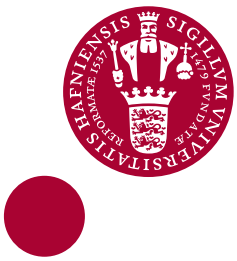

Transpiration and water budgets of European beech (Fagus sylvatica L.) dominated stands in relation to canopy structure

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FOREST & LANDSCAPE

Transpiration and water budgets of European beech (*Fagus sylvatica* L.) dominated stands in relation to canopy structure

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Paper I-V

1 English summary

In the future, it is likely that managed deciduous forests in Denmark will be characterized by single tree or group felling, creating gaps in the canopy. With time they may become heterogeneous in relation to tree species and size. This is in contrast to the earlier Danish even-aged management practices and use of mono-specific stands. These structural changes may affect the hydrological cycle in forest stands. The aim of this study was to relate some structural characteristics of mature European beech (*Fagus sylvatica* L.) dominated forests to their function in the water cycle. The results from case-studies on three European beech dominated mature forest sites are presented here. Two sites were conventionally managed, even-aged and monospecific stands (SOR_{MAN} and RAV_{MAN}) and one was an un-managed, uneven-aged and mixed natural forest reserve (SUS_{NAT}) with common ash (*Fraxinus excelsior* L.) and pedunculate oak (*Quercus robur* L.) in addition to European beech. Specifically, the study describes: i) the effects of gap formation on the hydrological cycle, ii) the effects of canopy stratification on European beech transpiration, and iii) the simulated water budget in a mixed uneven-aged and an even-aged monospecific forest. It was hypothesized that: (1) Relative to conditions in the closed forest, gap formation results in increased soil water storage, throughfall (precipitation falling through and from the canopy), soil water drainage, tree sap flow in gap edges and evapotranspiration from soil, litter and low vegetation; (2) solar elevation and wind direction as well as the proximity to and size of trees govern the spatial distribution of soil water storage and throughfall within a gap; (3) tree height and height distribution may influence tree and stand transpiration in European beech through the combined effects of gravity and a longer path length for water from soil to leaf for tall than for small trees; (4) simulated transpiration and interception loss in a mixed uneven-aged and a monospecific even-aged stand are the same due to the dominance of European beech in both stands. The process-based and one-dimensional simulation model CoupModel is parameterized and calibrated to estimate the hydrological budget for positions in the gap, at the gap edge and in the closed forest in two of the three stands studied (SUS_{NAT}, RAV_{MAN}). Gap diameters were ≤ stand height (D/H ≤1).

It was found that gap formation clearly increased soil water storage, throughfall and drainage, primarily in the growing season. Mean soil water storage in June-September was ≥90% of field capacity in gaps and 64-74% in the closed forest. Throughfall was up to 30% higher at gap than at closed forest positions in the period June-September. Throughfall in gaps equalled the precipitation (*P*) measured outside the forest in the first summer after gap formation. Throughfall did not differ among positions in winter where it was approximately 80% of *P*. Only very few measurements were available to describe forest floor evapotranspiration. In contrast to the expectations, they did not indicate any differences between the closed forest and the gap. Throughfall was not related to aspect within the gap and soil water storage relative to field capacity was slightly lower in the northern (0.93) than in the eastern (1.00) part of the

largest gap studied. A simple and spatial non-linear model ($R^2 = 0.43$, $p<0.0001$) relating measured soil water extraction to the stem basal area and position of trees predicted that water extraction by mature trees extends approximately 6-8 m from the tree. Annual simulated drainage (CoupModel) was 76-104% higher from gap positions (497-644 mm) than from closed forest positions (282-319 mm). Simulated drainage in the period November-April was relatively similar in gap (234-266 mm) and closed forest positions (188-235 mm). The application of the CoupModel in a daily time resolution in the complex setting of a small canopy gap indicated that the water use of trees at the gap edge may cause much of the variability in gap soil water storage observed during the growing season. This was supported by the spatial model (above) and by a graphical representation over time of the measured gap soil water storage in the growing season 2000. Further, the CoupModel application indicated that the water use of the vegetation in the gaps was very low regardless of the vegetation leaf area, presumably because of low incident radiation. The calibration of the CoupModel is best defined for positions in the closed forest. The application for edge and gap positions was useful to identify the importance of possible horizontal processes in the water cycle near a gap, but estimates in the water budget may be influenced by the inability of the model to reproduce these processes. During a seasonal soil drought, trees at the edge of a gap seemed to benefit from the availability of soil water with the result that they maintained relatively high sap flow rates throughout the summer 2000 in contrast to trees in the closed forest. In contrast to released subcanopy trees at the gap edge, sap flow rates for suppressed subcanopy trees and trees in the canopy were reduced by 29-39% during soil drought. Modification of the gap effect in the direction toward restoring the hydrological conditions of the closed forest was observed during the two years as growing season soil water storage in the gap edge was higher in the first year (2000) but similar to that in the closed forest by the second year (2001) after gap formation. This process is expected to continue for several years.

For the study on the effect of canopy stratification on transpiration, the individual tree mean stomatal conductance for trees 14-29 m tall as well as the canopy conductance (European beech only) for two stands differing in tree height distribution was calculated from sap flow measurements. In the present study, this hypothesis could not be verified, thus tree height does not influence transpiration on the sites used. European beech canopy conductance at a vapour pressure deficit (*vpd*) of 10 hPa was 0.01 and 0.008 m s^{-1} for the non-stratified (SOR_{MAN}) and the stratified (SUS_{NAT}) stand respectively. Total European beech transpiration was 203 mm (May 5-September 30) and 114 mm (June 15-September 30). For these two sites, it was observed that daily European beech canopy transpiration showed a constant relationship between the two stands (1:0.8 for the non-stratified and stratified stand respectively). The diurnal measurements showed that at high transpiration rates, the relationship was near 1:1 for the two stands, and it is suggested that the non-stratified canopy was subject to a slightly higher limitation in transpiration than the stratified canopy. This may possibly be due to the impact of

high *vpd*. To calculate transpiration from sap flow measurements the variation in sap flow with xylem depth is described. Sap flow decreased with increasing xylem depth measured on mature trees in the stratified stand. The observed decrease was moderate; at 50 mm xylem depth sap flow was approximately 50% of that observed in the outer xylem (0-20 mm). This may reflect deep roots or other tree characteristics not quantified in this study.

Simulations from the CoupModel showed that the mixed stand (SUS_{NAT}) had a slightly lower simulated annual transpiration (219-220 mm) than the monospecific stand (RAV_{MAN}, 241 mm), possibly due to the late leaf development of common ash and pedunculate oak as well as low transpiration rates of common ash. Lower transpiration due to other causes, as for example very high age and low vitality, were not investigated and they cannot be ruled out. The mixed stand had a higher simulated interception loss than the monospecific stand, partly due to low stemflow of common ash.

Based on the results of the present study, it is recommended to conduct more in-depth investigations of water budget and transpiration in relation to tree species, vitality and age. Future studies should include root distribution and functionality. High simulated as well as measured rates of evapotranspiration from soil, litter and low vegetation point to the need for further investigations on this process. The role of woody debris in the evaporation and storage of water should be investigated. Future studies on the water balance in gaps should include their effects on the hydrological cycle at the spatial level of the stand or the forest.

2 Dansk resumé

Fremtidig dyrkning af løvskov i Danmark vil være karakteriseret af enkelttræhugst og gruppevis foryngelse og dermed af etableringen af større og mindre lysbrønde i modne bevoksninger. På længere sigt kan skovstrukturen udvikle sig til at blive heterogen i relation til træart og træstørrelse. Dette står i kontrast til tidligere dyrkningsmetoder baseret på ensaldrede renbestande. De strukturelle forandringer kan berøre skovens hydrologiske kredsløb. Målet med dette studie var at undersøge relationer mellem udvalgte strukturelle egenskaber i bøgedomineret skov (*Fagus sylvatica* L.) og deres funktion i skovens hydrologiske kredsløb. Her præsenteres resultater fra undersøgelser (case-studier) i tre modne bøgedominerede skove. Lokaliteter er Lille Bøgeskov (SOR_{MAN}) og Ravnsholte Skov (RAV_{MAN}): ensaldrede og konventionelt drevne renbestande og Suserup Skov (SUS_{NAT}): urørt og uensaldret blandskov med ask (*Fraxinus excelsior* L.) og eg (*Quercus robur* L.) foruden bøg. Særlig beskrives: i) effekter af etablering af lysbrønde på det hydrologiske kredsløb, ii) effekter af stratificering af kronetaget på transpiration i bøg og iii) den simulerede vandbalance i en uensaldret blandskov og ensaldret renbestand. De opstillede hypoteser inkluderer: (1) Relativt til i lukket skov vil etablering af en lysbrønd resultere i højere jordvandindhold, gennemdryp (nedbør som drypper igennem og fra kronetaget), nedsivning fra rodzonen, kanttræers xylemsaftstrøm (sap flow) og fordampning fra skovbunden (jord, litter og lav vegetation); (2) solindstråling, vindretning samt afstand til og størrelse af træer påvirker den rumlige variation i jordvandindhold og gennemdryp i lysbrønde; (3) træhøjde påvirker transpirationen for bøg som følge af en længere vej fra rod til blad og en større effekt af tyngdekraften; (4) simuleret transpiration og interceptionstab i unsaldret blandskov og ensaldret renbestand er ens på grund af bøge-dominans på begge lokaliteter. Den prosess-baserede og en-dimensionale vandbalancemodel CoupModel benyttes til at estimere vandbalancer og er parameteriseret og tilpasset for lukket skov, lysbrønd og kant (overgang fra lukket skov til lysbrønd) i to af de tre skove. Diameteren på de undersøgte lysbrønde er ≤ bevoksningshøjden ($D/H \leq 1$).

Resultater viste at etableringen af en lysbrønd førte til højt jordvandindhold, højt gennemdryp og en større nedsivning relativt til i lukket skov. Primært i vækstperioden. Det gennemsnitlige jordvandindhold i juni-september var ≥ 90% af markkapaciteten i lysbrønde, men bare 64-74% i lukket skov. Gennemdryp var op til 30% højere i lysbrønde end i lukket skov i perioden juni-september. Gennemdryp i lysbrønde var lig nedbøren (*P*) målt udenfor skoven i løbet af den første sommer efter etablering af lysbrønden. Gennemdryp i vinterperioden var 80% af *P* uanset position relativt til lysbrønde. Kun få målinger beskriver fordampning fra skovbunden (jord, litter og lav vegetation). Mod forventning viste de ingen forskel mellem lukket skov og lysbrønd. Gennemdryp i lysbrønde adskilte sig ikke blandt positioner nord, syd, vest eller øst for lysbrøndens centrum. Jordvandindhold i sommerperioden relativt til markkapacitet var lidt lavere i den nordlige del (0.93) end i den østlige del (1.00) af den største lysbrønd. En simpel

ikke-lineær rumlig model ($R^2 = 0.43$, $p<0.0001$), som relaterer ændringer i målt jordvandindhold til stammegrundflade og position af træer, estimerede at vandoptag for store enkelttræer rækker 6-8 m fra stammen. Årlig simuleret nedsivning (CoupModel) var 76-104% højere fra lysbrønde (497-644 mm) end fra lukket skov (282-319 mm). Simuleret nedsivning i perioden november-april var relativt ens fra lysbrønde (234-266 mm) og lukket skov (188-235 mm). Tilpasningen af den en-dimensionale CoupModel i daglig tidsopløsning indikerede at vandoptag af træer i kanten er ansvarlig for en stor del af variationen i jordvandindholdet i lysbrønde henover vækstperioden. Dette støttes af en rumlig model (se ovenfor) og af en grafisk repræsentation of jordvandindhold i en lysbrønd over tid. Estimater fra vandbalancemodellen indikerede at vandoptag af vegetationen i selve lysbrønden var lav uanset den anvendte bladflade, hvilket kan være et resultat af lav lysindstråling i forhold til over bevoksningen. Tilpasningen af CoupModel er bedst defineret for forholdene i lukket skov. I lysbrønde og kanter kunne modellen bruges til at identificere mulige horisontale processer i det hydrologiske kredsløb, men modelestimaterne kan være påvirket af, at modellen ikke repræsenterer disse processer. Under gradvis udtørring af jorden i væksperioden nyder træer nær lysbrønden godt af højt jordvandindhold og høj vandtilgængelighed og kan opretholde en høj xylemsaftstrøm relativt til træer i den lukkede skov, som udviste faldende xylemsaftstrøm ved tiltagende udtørring af jorden. Effekten af lysbrønden på jordvandindholdet blev modificeret fra første til andet år efter etableringen, idet jordvandindholdet i vækstperioden for kanten var højere end i lukket skov i den første, men ikke i den anden sommer. Det forventes at effekten af lysbrønden vil forsvinde efter en årrække, men dette kunne ikke beskrives indenfor studiets tidsramme.

For at undersøge effekten af stratificering af kronetaget på transpiration blev den gennemsnitlige ledningsevne på bladniveau estimeret for enkelttræer med højde 14-29 m. Dertil blev ledningsevnen for kronetaget (bøg) estimeret for to bevoksninger med forskellig højdefordeling. Ledningsevne og transpiration blev beregnet fra målt xylemsaftstrøm. Den opstillede hypotese blev ikke verificeret og det konkluderes at træhøjden ikke påvirker transpirationen i bøg på de pågældende lokaliteter. Kronetagets ledningsevne (bøg) ved en damptryksdeficit (*vpd*) på 10 hPa var 0.01 og 0.008 m s^{-1} for henholdsvis den ikke-stratificerede og den stratificerede bevoksning. Målt total transpiration for bøg i den ikke-stratificerede bevoksning var 203 mm i perioden 5. maj-30. september og i den stratificerede bevoksning 114 mm i perioden 15 juni-30. september. Daglig transpiration (bøg) i den stratificerede bevoksning var 80% af transpiration i den ikke-stratificerede. Halvtimes målinger af transpiration for bøg viste, at ved høje transpirationsrater havde de to bevoksninger samme transpiration. Dette fortolkes som en mulig begrænsing i transpirationen for den ikke-stratificerede bevoksning, muligvis som en følge af at høj *vpd* resulterede i faldende ledningsevne. For at beregne transpiration fra xylemsaftstrømmen beskrives variationen i xylemsaftstrømmen relativt til xylemdybden i træstammer. Målt på træer i kronetaget faldt saftstrømmen med stigende xylemdybde, men faldet var mindre markant end i andre undersøgelser; ved en xylemdybde på 50 mm var saftstrømmen ca. 50% af strømmen målt

i de yderste 20 mm. Den radiale variation kan være påvirket af træernes roddybde eller af andre faktorer som ikke er kvantificeret i denne undersøgelse.

CoupModel-simuleringerne viste at blandskoven (alle arter incl.) havde en lavere årlig transpiration (219-220 mm) end den ensaldrede renbestand (241 mm). Dette kunne skyldes det relativt sene udspring for ask og eg og muligvis et lavt vandforbrug (lav xylemsaftstrøm) i ask. Andre mulige grunde kunne være høj alder og lav vitalitet, men dette blev ikke undersøgt. Blandskoven havde et højere simuleret interceptionstab end den ensaldrede renbestand, delvis på grund af et lavt stammenedløb i ask (nedbør som løber langs træstammen).

På grundlag af det gennemførte studie anbefales det, at effekter af træart, alder og vitalitet undersøges i relation til vandbalance og transpiration i skov. Fordeling og funktion af rødder bør være en del af disse studier. Målte og simulerede værdier af jordbundsfordampning var høje og bør undersøges videre og funktionen af dødt ved i forbindelse med fordampning og interceptionstab kunne indgå. Kommende undersøgelser af vandkredsløb i lysbrønde bør inkludere deres inflydelse på bevoksnings- og skov niveau.

3 Preface

This dissertation was written for the acquisition of the Ph. D. degree at The Faculty of Life Sciences, University of Copenhagen, Denmark (formerly The Royal Veterinary and Agricultural University). The study was carried out at the Danish Centre for Forest, Landscape and Planning (Forest & Landscape Denmark). Supervisors were Dr. forest et habil Jørgen Bo Larsen, Professor in silviculture, and Head of Research, Ph. D. Karsten Raulund-Rasmussen, Forest and Landscape Ecology. In 1999 and 2000, two research projects dealing with the ecology of European beech forests (*Fagus sylvatica* L.) were initiated. Spy-Nat-Force (Danish Research Council) and Nat-Man (EU 5th Framework programme). They focused on biodiversity and on soil chemical - and stand regeneration processes in natural and managed European beech forests when subject to small-scale disturbance. A third project initiated in 2000 (The influence of stand structure on forest water balance, microclimate and growth conditions, Danish Research Council) made it possible to investigate the water cycle in European beech forests in a higher temporal and spatial resolution than planned. This study has benefited from all three projects and two of the experimental sites (Suserup Forest and Ravnsholte Forest) were common. Inclusion of a third site (Sorø, Lille Bøgeskov Forest) was made possible by Teis Nørgaard Mikkelsen, Risø National Laboratory. The study commenced in 1999 and was interrupted by the births of my two daughters and when moving from Denmark to Norway. The study was financed by The Royal Veterinary and Agricultural University (now the Faculty of Life Sciences, University of Copenhagen), The Danish Centre for Forest, Landscape and Planning (now Forest & Landscape Denmark) and The Danish Agricultural and Veterinary Research Council. The dissertation was defended in Copenhagen on March 6, 2008 in the subject areas of forest ecology and forest hydrology. The examination committee consisted of Professor *Per Gundersen*, Forest & Landscape Denmark, University of Copenhagen (Chair), Directeur de Recherches, *Denis Loustau*, INRA, Centre de Bordeaux - Aquitaine, France and Associate Professor, *Helmut Schume*, University of Natural Resources and Applied Life Sciences (BOKU) Vienna, Austria. The dissertation is based on five papers of which two are published. Permission to include these was granted by the publishers. Manuscripts are referred to by their roman numerals and published articles by name and year.

I. Ritter, E., Dalsgaard, L., Einhorn, K.S. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management 206:15-33. (Ritter et al. 2005a).

II. Dalsgaard, L. 2007. Above and below ground gaps - the effects of a small canopy opening on throughfall, soil moisture and tree transpiration in Suserup Skov, Denmark. Ecological Bulletins 52:81-102. (Dalsgaard 2007).

III. Dalsgaard, L. Beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) sap flow in a natural deciduous forest in Denmark – interactions between forest dynamics and soil water variability near a canopy gap. (Paper III).

IV. Dalsgaard, L., Mikkelsen, T.N., Bastrup-Birk, A. Transpiration and canopy conductance of European beech (*Fagus sylvatica* L.) in a natural and a mature managed stand. (Paper IV).

IV. Dalsgaard, L., Bastrup-Birk, A., Schelde, K., Raulund-Rasmussen, K. Water budgets in a natural and a managed temperate deciduous forest - contrasting small canopy gaps and the surrounding closed forest. (Paper V).

4 Introduction

Forests interact with the local and regional water cycle. They provide clean water for human consumption and for streams and lakes because of low management intensity relative to e.g. agriculture (e.g. Callesen et al. 1999, Bastrup-Birk and Gundersen 2004). With their tall stature and their ramified canopy and root structure, they use water from the root zone, they buffer the run-off following precipitation events and counteract erosion (Hornbeck et al. 1997, Crockford and Richardson 2000, Granier et al. 2000a, Reubens et al. 2007). Trees depend on water for transpiration in order to grow and survive. They regulate transpiration to conserve the internal water content (Oren et al. 1999b). Severe drought, threatening the survival of trees or entire stands, are seldom (Peterken and Mountford 1996, Bréda et al. 2006), but low water availability for trees during the course of the growing season is frequent (Granier et al. 2000a, Pilegaard et al. 2001).

Forests cover 11% of the land area of Denmark (486.000 ha) and about one third is deciduous forest (Anon. 2002). During the last 20 years, the establishment of mixed deciduous forest has been promoted in areas where site conditions are suitable. In contrast to the previous dominating use of clear cutting systems and even-aged stands, it is now encouraged to aim for an uneven-aged stand structure and the use of natural regeneration following single-tree or group felling (Anon. 2002). In many aspects, the structure of managed deciduous forest could resemble that of a natural forest subject to small scale disturbances (Emborg et al. 2000). In addition to the structural changes in the existing forests, the forested area in Denmark is planned to double within a century (Anon. 2002). The high population density in Europe and intense agricultural management mean that only few natural forests still exist. Natural forests characterized by small scale disturbances make it possible to investigate the function of old forest ecosystems of high heterogeneity and they may act as an ecological reference for the relationship between structure and function, relationships that may apply in mixed uneven-aged managed forests (Hahn et al. 2007).

The water cycle in forests has been extensively investigated. Processes such as transpiration and interception loss on the stand scale are relatively well understood in mono-specific stands (e.g. Aussenac and Boulangeat 1980, Granier et al. 2000a, 2003, Thomsen et al. 2003) just like forest water balance simulations are numerous (e.g. Eckersten et al. 1995, Jochheim et al. 2004, Davi et al. 2005, Ladekarl et al. 2005, Christiansen et al. 2006). However, natural as well as managed uneven-aged deciduous forests may be characterized by a mixture of species, canopy stratification, a large range

in tree age and size, and by canopy gaps formed after felling or tree mortality. Information on the water relations of tree species not commonly applied in even-aged forest management (e.g. *Fraxinus excelcior* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Tilia cordata* Scop.) is relatively scarce (Hölscher et al. 2005). It is likely that these and other species will be introduced in mixed stands. Species differences in transpiration have been observed (e.g. Hornbeck et al. 1997, Oren and Pataki 2001, Wullschleger et al. 2001). Further, tree age and tree height may be determinants in some ecosystems (Schäfer et al. 2000, Roberts et al. 2001, Delzon et al. 2004, Delzon and Loustau 2005). In canopy gaps, the microclimate has been described (Gray et al. 2002, Ritter et al. 2005a) and the soil water storage in the growing season is often high in contrast to the surrounding stand. This can lead to a higher soil water drainage (Zirlewagen and von Wilpert 2001). However, studies of water fluxes in canopy gaps are quite few. Such gaps can make up close to 10% of the area in a natural deciduous forest (Emborg et al. 2000). The trees at the edges of these gaps may respond to high soil water availability with a higher transpiration than trees in the closed forest (Cienciala et al. 2002).

When considering mixed uneven-aged deciduous stands, the emerging questions relative to their water cycle include: i) What will be the consequence for the stand water budget of including a variety of ages and sizes of trees?, ii) What will be the effect of using species on which there is limited water related information in mixtures with already well-know species like European beech (*Fagus sylvatica* L.)? and iii) How does the water cycle in a canopy gap differ from that of the closed forest? To manage mixed uneven-aged forests to meet the demands from society related to the water resource as well as to ensure forest vitality under changing climatic conditions (Alcamo et al. 2007) answers to the above questions will be beneficial. The water cycle in natural forests may be useful in providing some of the answers and could also contribute to a more complete knowledge of the ecology of these diverse ecosystems.

In this study, some of the processes in the water cycle of European beech dominated forests are investigated. The aim is to relate some structural characteristics to their function on the spatial scale of a canopy gap and individual tree, as well as on the scale of the canopy and the stand. European beech is an important forest tree species in eastern Denmark, as well as in western and central Europe. The sites selected for this study represent even-aged mature mono-specific stands as well as a natural forest with European beech and common ash (*Fraxinus excelsior* L.) as the dominating canopy species. The water cycle in forests may be viewed as fluxes of water or water vapour directed to or from the storage compartments found mainly in the soil, litter and the vegetation surfaces (Figure 1).

In this study, fluxes illustrated in Figure 1 are estimated experimentally or by simulation (or both) in the closed stand, the canopy gap, and in the transition between the stand and the gap (gap edge) in a managed even-aged stand and in the natural forest. It was expected that the removal of the canopy, even in small gaps with diameter-to-height ratio (D/H) ≤1, would dramatically change the importance of the water fluxes relative to the closed stand. While the effects of the canopy gap are viewed as short-lived effects that may appear scattered throughout the stand following disturbance, any effect of the differences in the canopy structure, i.e. species and height distribution affects the entire stand in long periods. These effects are evaluated by simulation of the stand water balance as well as by calculated transpiration based on sap flow measurements.

Measuring fluxes of water and water vapour to and from stands of mature forests are often carried out in long term projects that demand large investments in canopy towers (e.g. Pilegaard et al. 2003). Such projects have ideal conditions for the characterisation of canopy processes under varying meteorological conditions. The present study relies predominantly on ground-based measurements obtained during two growing seasons, thus without canopy access and not covering meteorological extremes.

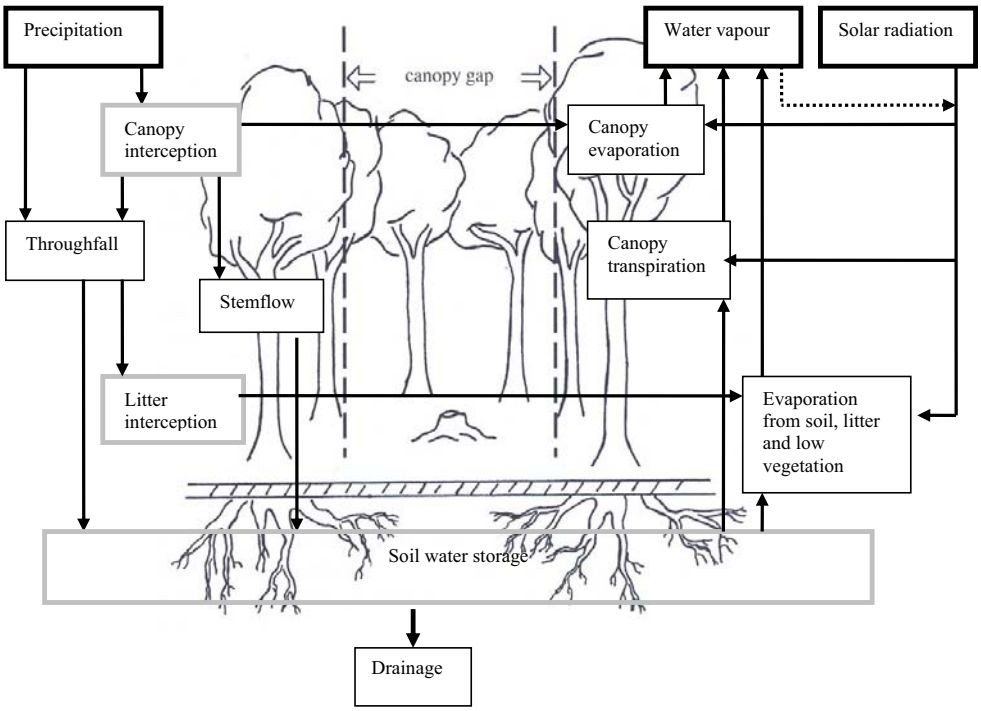

Figure 1. *The most important contributions in the hydrological cycle of a European beech dominated forest. Black arrows and thin-lined boxes illustrate fluxes of water and water vapour, thick black-lined boxes are forcing environmental variables and gray boxes illustrate water storage. While solar radiation forces evapotranspiration, the dotted line indicates that forcing is also linked to changes in vapour pressure. Redrawn from Ritter (2004) and Dufrêne et al. (2005).*

The thesis has the following structure: Hypotheses and how they are addressed in papers I-V are described in Chapter 5 followed by the description of study sites and measurement methods in Chapter 6. The environmental conditions and fluxes in a canopy gap are described in Chapter 7 from results in the present study as well as results from the literature. Chapter 8 deals with the transpiration and water cycle at the stand scale using results from the accompanying papers as well as from the literature. A final discussion of hypotheses, results and methods are found in Chapter 9 and conclusions and perspectives are given in Chapter 10. Figures, tables and equations are found in the accompanying papers when written in italics and in this presentation when written in normal font.

5 Hypotheses and accompanying papers

5.1 Hypotheses

Regarding the effects of the formation of a small canopy gap, the following hypotheses were addressed:

The formation of a small canopy gap (D/H ≤ 1) in the European beech dominated stands leads to increasing

> **A1** growing season soil water storage
> **A2** soil water drainage
> **A3** throughfall (precipitation falling through and from the canopy)
> **A4** evapotranspiration from soil, litter and low vegetation (forest floor)
> **A5** transpiration and xylem sap flow of trees in the gap edge - relative to those in the closed forest.

Paper I (Ritter et al. 2005a) presents preliminary results from the natural forest on gap, edge and closed forest soil water storage (**A1**) in 2000 and 2001. In paper II (Dalsgaard 2007), analyses are presented of the differences among closed forest, gap and edge soil water storage (**A1**), throughfall (**A3**) and evapotranspiration from the forest floor i.e. litter, soil and low vegetation (**A4**) in the natural forest. Results from the managed forest on soil water storage (**A1**) and throughfall (**A3**) in closed forest, edge and gap positions are found in Chapter 7 of this presentation. Transpiration and sap flow of trees near the gap in the natural forest (**A5**) are analysed primarily in paper III, but some results are shown in paper II (Dalsgaard 2007). In paper V, the simulation of water budgets for the managed and the natural stand in closed forest, edge and gap positions is presented and drainage is calculated (**A2**).

Further, hypotheses were formulated to test the influence of aspect in the gap (northern, southern, eastern, western part of gap) on soil water storage and throughfall as well as the influence of tree size (stem basal area) and position on water use at positions in and near the gap:

> **A6** Soil water storage is lower in the northern part of the gap than other parts due to high incident light.
> **A7** Throughfall is highest in aspects opposite to the prevailing wind direction; at the eastern and northern edges of the gap.

A8 The spatial distribution of water use measured from soil water storage at specific locations in and near the gap in the summer 2000 depends on the distance to the surrounding trees and their stem basal area.

A6 - **A8** are treated in paper II (Dalsgaard 2007) and in Chapter 7 of this presentation. An overview of results concerning **A1**-**A8** is given in Chapter 7 and the hypotheses are further addressed in Chapter 9.

Regarding transpiration and water budgets at the canopy and stand scale, the following hypotheses were addressed:

B1 Canopy conductance for mature European beech has a higher sensitivity to the air vapour pressure deficit (*vpd*) in the natural forest than in the managed forest due to the presence of small and intermediate size trees.
B2 The process-based water balance simulation model CoupModel (Jansson and Karlberg 2004) adequately represents the processes in the water cycle in European beech dominated mature forests as evaluated from comparisons of the predicted and observed soil water storage. Due to the dominance of European beech in both stands (natural and managed), it is expected that the simulated transpiration (governed by the calibrated value for the maximum stomatal conductance) and interception loss (calibrated to measured stemflow and throughfall volumes) is the same.

Analyses and results for **B1** are presented in paper IV and **B2** is treated in paper V. An overview of results concerning **B1** and **B2** is given in Chapter 8 of this presentation and the hypotheses are further addressed in Chapter 9.

5.2 Accompanying papers

Paper I Ritter, E., Dalsgaard, L., Einhorn, K.S. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. Forest Ecology and Management 206:15-33. (Ritter et al. 2005a).

This paper forms the background information on microclimate for several investigations in the natural forest gap. The objectives were to describe temporal and small-scale spatial variation in microclimate and soil moisture in and near a small canopy gap in a natural forest expecting an increase in light, soil moisture and soil- and air temperature after gap formation. The paper presents some of the results on gap, edge and closed

forest soil water storage in 2000 and 2001 as well as measurements of light and of soil- and air temperature conducted in the same gap.

Paper II Dalsgaard, L. 2007. Above and below ground gaps - the effects of a small canopy opening on throughfall, soil moisture and tree transpiration in Suserup Skov, Denmark. Ecological Bulletins 52:81-102. (Dalsgaard 2007).

This paper is a contribution to a book on Suserup Forest and the research that has been conducted there especially during the past 10-15 years. Differences in soil water storage, throughfall and forest floor evapotranspiration among closed forest, gap and edge positions in the natural forest are analysed. Stemflow measurements for European beech and common ash are presented. Using a non-linear model, the spatial variation in water use is estimated from measurements of soil water storage and individual tree basal area and position. Some results on tree sap flow and transpiration for trees in the closed forest and in the gap edge are shown.

Paper III Dalsgaard, L. Beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) sap flow in a natural deciduous forest in Denmark – interactions between forest dynamics and soil water variability near a canopy gap.

Individual tree measurements of sap flow are presented for European beech and common ash in the natural forest during the summer 2000. Transpiration is calculated for European beech. It is hypothesized that during a seasonal soil drought, trees near the gap will benefit from the high availability of soil water resulting in a higher sap flow and transpiration than trees in the closed forest. Further, it is hypothesized that small trees below the main canopy in the closed forest experience the strongest limitations to transpiration and sap flow. The observed variation in sap flow with increasing xylem depth in European beech stems used for the calculation of tree and canopy transpiration is described.

Paper IV Dalsgaard, L., Mikkelsen, T.N., Bastrup-Birk, A. Transpiration and canopy conductance of European beech (*Fagus sylvatica* L.) in a natural and a mature managed stand.

European beech transpiration and canopy conductance (g_c) are compared for a natural and a managed stand calculated from simultaneous sap flow measurements in 2000. It is hypothesized that European beech g_c will be more sensitive to changes in *vpd* in the natural stand than in the managed stand. Mean stomatal conductance for trees 14-29 m height is calculated from sap flow measurements to investigate the relationship between

a reference mean stomatal conductance and tree height. The hypothesis rests upon results from Schäfer et al. (2000) showing that in European beech, higher mean g_s and a higher sensitivity to *vpd* can be expected in small trees than in tall trees. This is suggested to result from the effects of gravity and a longer flow path in tall trees combined with the maintenance of a minimum leaf water potential (Ryan et al. 2006).

Paper V Dalsgaard, L., Bastrup-Birk, A., Schelde, K., Raulund-Rasmussen, K. Water budgets in a natural and a managed temperate deciduous forest - contrasting small canopy gaps and the surrounding closed forest.

Objectives are to apply the one-dimensional process-based CoupModel in the heterogeneous setting of a small forest canopy gap and to calculate the water budget in closed forest, gap and gap edge in two mature European beech dominated forests. It is hypothesized that drainage is high in gaps, intermediate in gap edges and lowest in the closed forest and that simulated transpiration and interception loss in the two forests were similar due to the dominance of European beech. Data used in model calibration include data shown in paper II and Chapter 7 of this presentation.

6 Study sites and measurement methods

6.1 Study sites

The three study sites are situated in the central part of Zealand, Denmark (Figure 2). Mean annual air temperature is 8.1°C with a minimum monthly mean of 0.8 °C in January and a maximum monthly mean of 16.7 °C in July and August (Danish Meteorological Institute DMI 1987-1997 station 29271, Laursen et al. 1999). Mean annual precipitation is 635 mm in Ravnsholte Forest, 644 mm in Suserup Forest and 668 mm in Sorø (DMI 1961-1990, Frich et al. 1997). Soils are predominately loamy till developed from calcareous parent material from the Weichselian glaciation and for Ravnsholte, Suserup and Sorø respectively they are further described by Ritter et al. 2005b, Ritter and Vesterdal 2006 and Pilegaard et al. 2003. No hard soil layers restrict the potential root depth but a high ground water table was observed in Sorø during winter (Ladekarl et al. 2001).

Study sites:

1 Suserup Forest, 55°22´N, 11°34´E (Ritter et al. 2005a, Dalsgaard 2007, paper III, IV, V)

2 Ravnsholte Forest, 55º31'N, 11º54'E (paper V)

3 Sorø, 55º29'N, 11º38'E (paper IV)

Figure 2. *The location of sites for the study of the hydrological cycle in European beech dominated forests in eastern Denmark, 2000-2001. Measurements from the sites contribute to papers I-V as shown to the right.*

Suserup Forest (*SUS*$_{NAT}$) is a narrow strip of forest located along the northern shore of Tystrup Lake. The 19.2 ha forest is a reminiscence of the natural mixed deciduous forest in the area. In a European context, human impact has been low since approximately 900 A.D. (Fritzbøger and Emborg 1996, Hannon et al. 2000, Heilmann-Clausen et al. 2007).

The forest is a mosaic of different tree sizes and species and is characterized by a number of small canopy openings (<1200 m^2) formed after wind-throw or single tree mortality. The structure and dynamics are described in detail by Emborg et al. (1996, 2000). Pedunculate oak (*Quercus robur* L.) is found as a few large individuals and Wych elm (*Ulmus glabra* Huds.) as saplings. European beech and common ash are the dominating canopy species. Lime (*Tilia platyphyllos* Scop.) and sycamore maple (*Acer pseudoplatanus* L.) are found in some parts of the forest. Measurements were concentrated in and near an irregularly shaped canopy gap created in a hurricane in December 1999. On this occasion, a number of trees were wind-thrown and a large old European beech tree lost most of its crown.

The Sorø site in Lille Bøgeskov Forest (SOR_{MAN}) is an even-aged managed stand and measurement facilities, including a canopy tower, contribute to the network measuring forest gas exchange in Europe (Pilegaard et al. 2003). Flux measurements from the tower are not used in the present study.

Ravnsholte Forest (RAV_{MAN}) is an even-aged managed stand. Saplings and regeneration of sycamore maple are found at the site. Measurements were obtained in or near a nearly circular canopy gap created by felling in January 2001. Stand structure parameters and stem diameter distributions for the three sites are summarized in Table 1 and Figure 3. Appendix 1 contains photos taken at the sites.

In SUS_{NAT}, the vegetation in the gap was dominated by regenerating European beech and common ash (Ritter et al. 2005a). In October 2000, regeneration height was approximately 0.3 m and in June 2002, common ash regeneration had reached a height of 1.5 m. The highest density as well as the tallest regeneration was found in the central and northern parts of the gap. In RAV_{MAN}, scattered advanced regeneration of sycamore maple was present (Ritter 2004, Ritter et al. 2005b).

Table 1. *Stand structure on three sites in Denmark where studies of the hydrological cycle in mature European beech dominated forest were conducted 2000-2001. For Sorø, data are from Pilegaard et al. (2003) and Mikkelsen (unpubl. data). In Suserup, stand structure was described on a 0.64 ha reference plot and in Ravnsholte on a 0.42 ha reference plot. Threshold stem diameter was 45 mm. For Suserup and Ravnsholte the reference plot surrounded the gap and the area in the gap opening was not included in the calculation of the stand basal area. In Suserup, tree height was measured on all trees, in Ravnsholte 60 trees were measured. LAI is the leaf area index. SE is the standard error of the mean.*

	Suserup unmanaged	Sorø managed	Ravnsholte managed
Basal area (m^2 ha^{-1})	40.2	29	28.5
Tree species (basal area in %)	*Fagus sylvatica* L. (56) *Fraxinus excelsior* L. (28) *Quercus robur* L. (13) *Ulmus glabra* Huds. (3)	*Fagus sylvatica* L. (89) *Picea abies* (L.) Karst.(2) *Quercus sp.* (2) *Larix sp.*(6) *Fraxinus excelsior* L. (1)	*Fagus sylvatica* L. (95) *Pseudotsuga menziesii* (Mirb.) Franco (2) *Larix sp.* (3)
Stand density (*n* ha^{-1})	733	283	304
Mean tree height (m)	13.3 (SE=0.4, *n*=463)	25±1[2]	23.1 (SE=1.0, *n*=60)
[1]Top height (m)	28.4 (SE=0.4, *n*=64)	-	28.9 (SE=0.2, *n*=20)
Mean tree diameter (m)	0.18 (SE=0.01, *n*=466)	0.38 (SE=0.01, *n*=57)	0.31 (SE=0.01, *n*=110)
Stand age (years)	280[4]	80	75
LAI (m^2 m^{-2})	4.6[3]	4.2[3]	4.0[3]
Gap diameter (m)	20	-	27

[1] Mean height of the 100 tallest trees ha^{-1}.

[2] Observed canopy height from the tower (Mikkelsen, pers. comm.).

[3] Measured 1 m above the ground with the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA) in late August 2000 (Suserup), late August - late September 2000 (Sorø) and in late June 2001 (Ravnsholte).

[4] Oldest European beech trees are approximately 280 years (Emborg et al. 2000) and forest continuity is long.

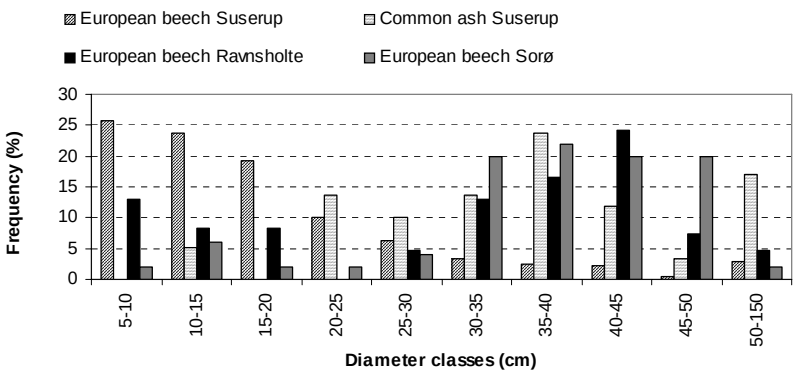

Figure 3. *Stem diameter distribution at the Sorø site and in Suserup and Ravnsholte forest. Stem diameter was measured 1.3 m above the ground (Suserup and Ravnsholte) or at approximately 1.6 m above the ground (Sorø).The number of observations on each site is 50 (Sorø), 108 (Ravnsholte) and 275 and 59 (Suserup, European beech and common ash, respectively).*

6.2 Measurement methods

6.2.1 Meteorological measurements

Photosynthetic active radiation (*PAR*, µmol m^{-2} s^{-1}), air temperature (T_a, °C), relative air humidity (*RH*, %), wind speed (*u*, m s^{-1}) and precipitation (*P*, mm) were measured using standard equipment and logged automatically (see paper III and IV, Pilegaard et al. 2003 for details on the instruments used). In SUS_{NAT} and RAV_{MAN}, measurements were 2 m above the ground with a station above a fallow field (SUS_{NAT}) or newly planted forest (RAV_{MAN}) approximately 300 m north of the measurement sites (*PAR*, T_a, *RH*, *u*, *P*) and a station in the forest below the canopy (T_a, *RH*, *u*). In SOR_{MAN}, measurements were obtained from the canopy tower 25-57 m above the ground. Measurements of *P* were corrected for the effects of wind and wetting (Vejen et al. 2000).

6.2.2 Throughfall and stemflow volumes

In SUS_{NAT} and RAV_{MAN}, volumes of throughfall (*P* falling through or from the tree crowns) were measured manually using funnels mounted 1 m above the ground in and near the canopy gaps (Dalsgaard 2007, paper V). Collection bottles were buried and measurements were corrected for wetting (Vejen et al. 2000).Though throughfall in the centre of the gaps approached that of *P* measured outside the forest, it is still termed throughfall and considered to be influenced by the forest canopy. At the same two sites volumes of stemflow (*P* reaching the ground by running down the tree stems) were recorded manually by collecting the water from a silicon collar spiraled twice around the tree stems (Dalsgaard 2007, paper V). Throughfall and stemflow volumes in SOR_{MAN} are not reported.

6.2.3 Sap flow

In SUS_{NAT} and SOR_{MAN}, the upward water transport through the xylem (sap flow) was measured using the thermal dissipation technique (Granier 1985, 1987, Granier et al. 1996) (paper III, IV). All probes were 20 mm long and 2 mm in diameter (in SUS_{NAT} constructed by ProBit, Freiburg, Germany). Two probes were installed radially into the tree stem and placed with a vertical distance of 0.1 - 0.2 m. The upper probe was heated by a constant current of 120 mA. The temperature difference between the probes was automatically and continuously logged and later converted, using an empirical calibration function (Granier 1987), to a water flux density J_s ($g_{water}\ m^{-2}{}_{xylem}\ s^{-1}$):

Eq. (1) $$J_s = 119\ [(\Delta T_0/\Delta T)-1]^{1.23}.$$

ΔT (°C) is the temperature difference between the two probes and ΔT_0 is the temperature difference when there is no sap flow i.e. at night. In SUS_{NAT}, the program *DATAMAN* (Ce Huang 1993, version 1.03) was used for the calculation of J_s and in SOR_{MAN} calculations were made in an excel spreadsheet. Installations were covered to prevent heating and water intrusion. In SOR_{MAN}, installation, data acquisition and calculation of J_s were conducted by Teis N. Mikkelsen (Pilegaard et al. 2003).

6.2.4 Soil water content and soil water retention

The volumetric soil water content (*SWC*) was measured using the Time Domain Reflectometry (*TDR*) method (Topp et al. 1980) on vertically installed stationary probes and calculated according to the calibration equation from Topp et al. (1980).

Eq. (2) $$\theta_v = -5.3 \cdot 10^{-2} + 2.92 \cdot 10^{-2} \cdot K_a - 5.5 \cdot 10^{-4} \cdot K_a^2 + 4.3 \cdot 10^{-6} \cdot K_a^3,$$

where θ_v is the volumetric soil water content ($m^3\ m^{-3}$) and K_a is the apparent dielectric constant of the soil volume. In SUS_{NAT} and RAV_{MAN} (Ritter et al. 2005a, Dalsgaard 2007, paper V), the calculation was imbedded in the software *AUTOTDR* (Thomsen 1994) and measurements were carried out manually with a cable tester (Tektronix, 1502C/1502B, Tektronix Inc., Berkshire, UK). They were conducted biweekly during the growing season and less frequent (approximately monthly) in the remaining periods. Probes extended 0.90, 0.50, 0.30 and 0.14 m into the soil from the undisturbed soil surface.

In February 2001, the gravimetric soil water content (SWC_G) was compared to simultaneous *TDR* measurements of *SWC* in SUS_{NAT} (Dalsgaard and Ritter, unpublished data). In a soil pit east of the canopy gap (Ritter and Vesterdal 2006), six samples (78.5-82.3 cm^3) in each of four soil horizons were obtained for the determination of SWC_G (fresh weight – dry weight, 1 week, 60°C). In each horizon, the horizontal *SWC* was measured with four probes of 0.20 m length. The mean values are shown in Table 2. In horizons A and E, *TDR* measured *SWC* overestimated SWC_G by 6 and 13%. In C, the largest sampling error was observed and *TDR* measured *SWC* underestimated SWC_G by 11%.

Table 2. *Soil water content (vol.%) in Suserup determined gravimetrically (SWC_G) and by horizontal TDR measurements (SWC). The standard error of the mean (SE) is given.*

Horizon	Depth (m)	SWC_G (SE)	SWC (SE)
A	0-0.2	31.0 (1.9)	32.7 (0.9)
E	0.2-0.33	24.2 (1.5)	27.5 (0.8)
B_t	0.33-0.41	25.9 (0.9)	25.9 (1.4)
C	0.41-	27.3 (2.1)	24.4 (2.9)

SWC_G was used to calculate the mean vertical *SWC* integrated over a 0.90, 0.50, 0.30 and 0.14 m profile ($SWC_{G\text{-}V}$). These were compared to vertical *TDR* measurements (n = 4) in identical depths placed within 1 m of the soil pit. The mean values are listed in Table 3. In 0-0.14 and 0-0.30 m depth, vertical *TDR* measured *SWC* overestimated $SWC_{G\text{-}V}$ by 19 and 3%. In 0-0.50 and 0-0.90 m depth, the vertical *TDR* measured *SWC* underestimated $SWC_{G\text{-}V}$ by 6 and 11%.

Table 3. *Soil water content (vol.%) as the mean integrated vertical profiles in Suserup determined from gravimetrical measurements ($SWC_{G\text{-}V}$) and by vertical TDR measurements (SWC). The standard error of the mean (SE) is given.*

Profile depth (m)	$SWC_{G\text{-}V}$ (SE)	SWC (SE)
0-0.14	31.0 (1.9)	36.9 (1.3)
0-0.30	28.7 (3.0)	29.5 (0.9)
0-0.50	27.8 (2.3)	26.0 (0.5)
0-0.90	27.6 (12.5)	24.5 (2.3)

The two comparisons showed that the *TDR*-method tends to overestimate the gravimetrically determined soil water content in the A and E horizons on this study site. The calibration formula in Eq. (2) is developed for relatively sandy soils (Topp et al. 1980) and may not represent the humus-rich upper soil in the forest. However, it was not possible to introduce a general correction of *TDR* measured *SWC*. The C horizon was characterized by a sandy matrix with the occasional inclusion of clay which introduced a large variability in SWC_G. Further, Rajsek (unpublished data) found a high variability in the thickness of soil horizons in and near the gap. Because of heterogeneity in soil properties, it was expected that the variability in *TDR* measured *SWC* would be high. Conclusions are that the highest confidence should be given to the three deepest vertical *TDR* measurements and that a deviation of 11% from the values estimated from gravimetrical measurements is acceptable in this heterogeneous soil. It is assumed that this comparison is representative also for RAV_{MAN}. Soil water retention was measured in the laboratory on samples from two soil pits in SUS_{NAT} and in one soil pit in RAV_{MAN} (paper V, Schjønning 1985). Data are summarized in Appendix 2. In-situ field capacity was estimated as the mean of measurements January 25 - April 24 (some positions April 19). In SOR_{MAN} (paper IV), *TDR*-measurements were automated. Details are reported by Ladekarl (2001) including a comparison of gravimetric- and *TDR* measured soil water content.

6.2.5 Evapotranspiration from the forest floor

Daily evapotranspiration from the forest floor (soil, litter and for some samples low vegetation of approximately 0.25 m height) was measured with small lysimeters at three occasions in SUS_{NAT} and two occasions in RAV_{MAN} (Dalsgaard 2007, paper V). Because of frequent small showers during these periods only a few of the data are reported.

6.3 Sampling and scaling

In SUS_{NAT} and RAV_{MAN}, measurements of ***SWC*** and **throughfall** were conducted in a grid or transect spanning across the canopy gap and reaching into the adjacent closed forest (Ritter et al. 2005a: *Figure 1*, Dalsgaard 2007, paper V: *Figure 1*). A total of 59 measurement positions were established in SUS_{NAT} in 2000, n=13 in gap, 29 in closed forest, 17 in the edge. In 2001 the number of positions was reduced to 28: n=10 in gap, 10 in closed forest, 8 in the edge. 28 positions were established in RAV_{MAN} in 2001: n=12 in gap, 12 in closed forest, 4 in edge. *SWC* and throughfall was averaged for positions in the canopy gap, the closed forest and the edge. **Forest floor evapotranspiration** was measured with a total of 16 samples; n=8 in gap positions (± low vegetation) and in the closed forest (± low vegetation). **Stemflow** was measured only in the closed forest, in SUS_{NAT} on 10 trees (European beech, common ash) and in RAV_{MAN} on three (European beech) (Dalsgaard 2007, paper V). Sample trees were outside the area where *SWC* was measured. A stand estimate of stemflow was calculated based on tree basal area. Two of the trees in SUS_{NAT} were in the edge of a nearby canopy opening and showed higher stemflow than trees in the closed stand.

Sap flow was measured on 20 trees (European beech, common ash) in SUS_{NAT} (paper III: *Figure 1 and Table 2*, paper IV) and on 12 trees (European beech) in SOR_{MAN} (paper IV). Trees were chosen to represent the diameter distribution of the stands within the practical constraint of e.g. cables length. Sap flow from two of the European beech trees in SUS_{NAT} showed erroneous data from the beginning of the measurement period and were not included in the study. Both were understorey trees; one showed very low J_s and it was found that the probe had been placed in an old wound and the other showed extremely high values of J_s. In SUS_{NAT}, measurements in 2000 were in the outer 20 mm of the xylem. Sap flow in the xylem beyond 20 mm was described in a study in 2001 in SUS_{NAT} where sap flow was measured to a xylem depth of 60 mm (paper III). In SOR_{MAN}, measurements were in 0-20 mm and 20-40 mm xylem depth and sap flow beyond this depth was estimated from results in the literature. Canopy transpiration was derived from sap flow using a weighted average (SUS_{NAT}) or a mean of all trees (SOR_{MAN}) (paper IV). Canopy conductance for European beech was calculated by inverting the Penman-Monteith equation (paper IV, *Eq. (1)*). In SUS_{NAT}, sap flow sensors were left in the trees during the winter 2000-2001. This proved to be unfortunate since the sap flow data from 2001 were in error (many extremely high rates with no apparent explanation) and data were not used. Further, sap flow for common ash could not be scaled properly to the tree and stand level (paper III). Sensors measuring sap flow to a xylem depth of 60 mm were installed in 2001 thus not subject to these errors, but measurements were constrained to 8 days in July. An attempt was

made to estimate sap wood area (estimating wood water content; fresh weight - dry weight, 24 hours, 103°C) in small sections of extracted wood cores from European beech and common ash, but was not successful. Sap flow measurements in RAV_{MAN} were not successful.

6.4 Experimental approach and the application of the CoupModel

The three selected sites do not represent different experimental treatments of identical units. Rather they are parallel case-studies where certain processes in the forest water cycle are investigated. The natural forest is not regarded as a future version of the managed stands after a period in structural transition. Thus, this study cannot determine difference in the water cycle between managed and natural forests nor the change in the water cycle as management converts homogeneous stands into forests resembling natural forests. As case-studies, they are meant to contribute to the development of hypotheses which may be tested using larger and more representative samples. The site referred to as a natural forest (Suserup Forest) has been subject to management in periods during history, thus it is not a virgin forest. In other contexts, the forest has been described as a semi-natural forest or a near-natural forest. The edge is long relative to the forest area and the forest may be affected by the microclimate in the surroundings. The two gaps studied are small (≤ stand height) and the present study does not intend to describe the possible effects of gap size on the water relations of either the gap itself or the whole stand - though the issue may be discussed. A gap is considered a time limited opening in the forest canopy after the mortality of one or several canopy trees. Single tree gaps often cover near 100 m^2 and multi-tree gaps 400-1000 m^2 (Canham et al. 1990, Coates and Burton 1997). The two gaps in the present study are small multi-tree gaps and the gap area is assumed to be outlined by the edges of crowns surrounding the gap.

In this study, canopy and stand scale processes (paper IV, V) and processes relating to the transition from closed forest to canopy gap (Ritter et al. 2005a, Dalsgaard 2007, paper III, V) are investigated. Measurements in the gaps were initiated in the first growing season after their formation. This means that results cannot be compared to pre-gap conditions and therefore a direct effect of this disturbance cannot be observed. In any reference to a gap effect, it is assumed that the pre-gap conditions equal the conditions observed in the closed forest. This is similar to Gray et al. (2002). Measured tree height was used quantitatively in some analyses, but the relationship between tree height and tree age in the stands was not subject to investigation. Any reference to tree age in SUS_{NAT} is based on the personal observations of large and possibly declining trees and the special history of this site. Data were evaluated using ANOVA and linear-

or nonlinear regression using the GLM and NLIN procedures in SAS version 8.1 and 8.2 (SAS Institute, Cary, NC).

Water budgets were simulated for one year in RAV_{MAN} and two years in SUS_{NAT} using the CoupModel (Jansson and Karlberg 2004) calibrated to measured soil water storage, throughfall and stemflow (paper V). Simulations were carried out for closed forest, gap and gap edge positions with input of reference climate representing above canopy conditions and gap climate representing microclimate in the small canopy gaps. The CoupModel simulates infiltration *to* and transpiration, evaporation and drainage *from* a layered soil in one dimension (Figure 4). The central part of the model consists of two coupled differential equations for water and heat flow solved by an explicit numerical method. The model was used in a daily time resolution with the plant canopy represented by a single big leaf. Soil evaporation (evaporation from the forest floor) was calculated with an iterative surface energy balance approach. The hydraulic soil properties used the Brooks and Corey representation of the retention curves and the Mualem representation of hydraulic conductivity based on measured soil water retention (Appendix 2). The soil column was divided into 16 layers with a lower boundary at 2.5 m depth. The canopy surface resistance was calculated using the Lohammer equation. Canopy surface properties were given as parameters (albedo, height, *LAI*) or calculated from height (displacement, roughness). Rooting depth was given as parameters and root distribution with depth was exponential. Water uptake was flexible among soil layers.

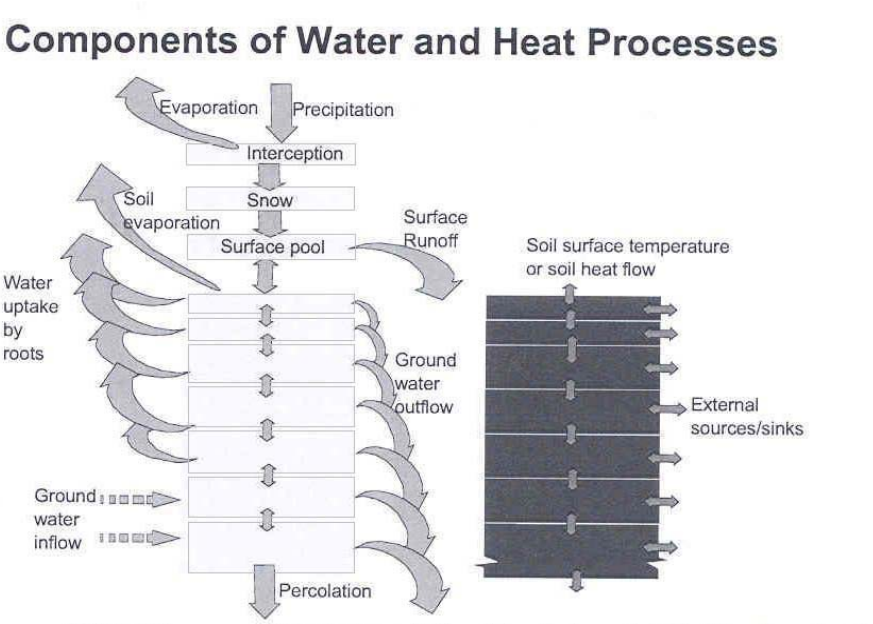

Figure 4. *Mass balance (left) and heat balance (right) of the CoupModel. From Jansson and Karlberg (2004).*

7 Microclimate and water flux in small canopy gaps

7.1 The importance of gap formation

Gaps are formed in natural as well as in managed forests after natural mortality or felling of one to several canopy trees. The most obvious result of gap formation is an increase in light at the forest floor. In many temperate forests light is an important limiting factor for the survival and growth of regeneration (Emborg 1998, Szwagrzyk et al. 2001). Gap formation is therefore essential to the cyclic succession of natural forests (e.g. Emborg et al. 2000) and as a silvicultural tool during stand regeneration (Coates and Burton 1997, Aussenac 2000). Gap formation can result in increased amounts of N (nitrate, ammonium) in the soil solution (Bauhus and Bartsch 1995, Ritter et al. 2005b, Ritter and Vesterdal 2006) and changes in the N-cycle and decomposer community (Ritter and Bjørnlund 2005) due to increased heat flux and a reduction in the vegetation cover. Regeneration and mineral cycling are central ecosystem processes and they both interact with the water cycle. Seedling growth depends on the availability of soil water (Madsen 1994, Madsen and Larsen 1997), and the mass flow and cycling of nutrients are determined in part by the fluxes of water. In this chapter, the physical environment in a small canopy gap is described. Results on the variability in soil water content (*SWC*) and the water fluxes in and near such a gap are presented i.e. throughfall, stemflow, tree transpiration and sap flow, forest floor evapotranspiration and simulated drainage and water budget.

7.2 The physical environment in a small canopy gap

7.2.1 Incoming radiation

Below the canopy in a temperate deciduous forest, the ground may receive less than 5% (Madsen and Larsen 1997) or less than 2% (Emborg 1998) of average incident *PAR* in the growing season. The opening of the forest canopy allows light to penetrate to the forest floor. In a Northern hardwood forest (39.6°N), Canham et al. (1990) found that, integrated over the growing season, a maximum of 17% of incident *PAR* was observed in the northern edge of a 20 m diameter gap (D/H: 2/3). A minimum of 5% was found in the southern gap edge. In the centre of small gaps (D/H: 2/3-1), 8-14% of incident solar radiation was reported (Aussenac 2000) and 10-18% in the northern gap edges. Thus, the path of the sun and the geometry of the trees result in a displacement of the zone of maximum light from the gap centre toward the north. This pattern in the spatial variability of light is a result of direct beam radiation and is typical for the Northern

hemisphere. Diffuse light which prevails in cloudy conditions is governed mostly by the structure of the canopy (Ritter et al. 2005a). When released saplings are maintained in the gap, this pattern can be changed (Ritter et al. 2005a) and the overall spatial variability becomes less predictable. A spatial average for 2000 and 2001 in the gap in SUS_{NAT} showed that *PAR* was 15-20% (mid-summer) and 15-16% (October) of incident *PAR* (Ritter et al. 2005a). These estimates include an overestimation of approximately 10% relative to the incident *PAR* measured with a horizontal diffuser because sensors in the gap used spherical diffusers (Einhorn pers. comm.). In spite of the dramatic increase in light, the environment at the ground in small canopy gaps is still characterized by relative darkness compared to the light environment found above the forest. Potentially, the centre of gaps in Northern hardwood forests (D/H: 2/3-1) may receive on average 2-3 hours of direct sunlight each day of the growing season (Canham et al. 1990).

7.2.2 Air temperature, soil temperature, humidity and wind

Because of incoming radiation, T_a generally reaches a higher maximum during the day in a small gap than below the canopy of a closed forest. A midday excess of 2°C was found at 10 cm above the ground in the centre of gaps with D/H of 0.85-0.93 (Geiger 1941 in Geiger et al. 1995). Ritter et al. (2005a) found that maximum T_a in the gap centre in SUS_{NAT} was up to 10°C higher than remaining plots. At night, radiation losses from the gap will result in a lower T_a than below the closed forest canopy. During cold spring nights, T_a was up to 2°C lower in small gaps (D/H ≤ 1) than below the closed canopy (Geiger 1941 in Geiger et al. 1995). In small gaps, the warm air from below the closed canopy will usually dominate night time T_a keeping the effect of radiative cooling relatively low. Mean daily T_a in the gap centre on sunny summer days were not different among gap sizes (D/H ≤ 1) or between gap and control plots in a temperate coniferous forest (Gray et al. 2002) whereas Ritter et al. (2005a) found that daily mean T_a in SUS_{NAT} was up to 5°C higher in the centre of the gap than below the closed canopy. In the latter study, the sensors were shaded by relatively small radiation shields which may have resulted in high temperatures.

Monthly averages of the daily mean and maximum soil temperature in the gap in SUS_{NAT} was up to 3°C higher in the centre of the gap than in positions with statistically different soil temperatures (Ritter et al. 2005a). Positions with high soil temperature were found in the central and southern parts of the gap and, especially during May-August, in the closed forest east of the gap. Thus, the soil in the northern part of the gap in SUS_{NAT} was cooler than that in the gap centre, and this was suggested to be caused by the evaporative cooling in the northern part of the gap through transpiration by the dense regeneration. In contrast, Gray et al. (2002) found that soil temperatures in the

gap increased from the southern to central to northern parts, specifically in gaps with D/H of 0.4-1.0. This was explained by high direct incoming radiation and by the fact that dry soil conditions in the northern part of large gaps could have promoted the high temperatures.

Potentially, turbulent large scale eddies can develop in a gap or clearing (Wrede 1925 in Geiger et al. 1995) possibly resulting in a higher wind speed (u) in gaps than below the closed forest canopy. u near a small gap in SUS_{NAT} was generally below 1 ms^{-1} in periods where open-field u was up to 8 ms^{-1} (paper IV), indicating that the gap did not induce high u. This is supported by the general notion that the high diurnal maximum T_a in the centre of small gaps is maintained through the low mixing of air in these small gaps (Geiger et al. 1995). The relative air humidity will increase with decreasing temperature observed as dewfall at night, and decrease with increasing temperature in the daytime.

7.2.3 Soil water content

In temperate forests, the formation of a small gap generally results in gap soil water storage near field capacity through the growing period while it decreases below the closed canopy (i.e. Bauhus and Bartsch 1995, Gray et al. 2002, Ritter et al. 2005a). In this study, the spatial and temporal development of differences in closed forest and gap *SWC* is illustrated in *Figure 5* (Dalsgaard 2007) where *SWC* in the gap centre in SUS_{NAT} is near field capacity throughout the summer 2000, but the water consumption of the closed forest results in decreasing *SWC* in the gap edges toward the end of the summer. For SUS_{NAT} and RAV_{MAN}, *SWC* measured in 0-0.90 m depth was high throughout the measurement period in the gaps, but decreased in the growing season both in the forest and at the edges of the gaps (paper V: *Figure 3*). Results on *SWC* relative to field capacity (SWC_{REL}) for closed forest, edge and gap positions in SUS_{NAT} showed for seasonal means, that edges were significantly different from other positions in the first summer after gap formation, but in the second summer, edge positions were not different from the closed forest (Dalsgaard 2007: *Table 3*). In RAV_{MAN}, edge and closed forest SWC_{REL} differed in summer and autumn in 0-0.90 m depth but were similar in 0-0.30 m depth (Table 4). In general for both gaps, *SWC* and SWC_{REL} were significantly higher for gap than for closed forest conditions in summer and in autumn except autumn *SWC* in RAV_{MAN} 0-0.90 m depth.

Table 4. *Mean and standard error of soil water content (SWC) in the intact forest, edge and canopy gap for Ravnsholte Forest, Denmark in 0-0.30 and 0-0.90 m soil depth, measured in 2001. Different letters indicate significant ($p<0.05$) differences among categories in a Bonferroni-adjusted t-test. Measurement methods are described in Dalsgaard (2007) and paper V. FC is field capacity. * indicate that the response variable was transformed for the analysis, but the mean and standard error shown are based on the original observations.*

SWC	0-0.90 m			0-0.30 m		
(vol.%)	Forest	Gap	Edge	Forest	Gap	Edge
Apr-May	^{AB}25.3(0.7)	^{A}27.0(0.6)	^{B}23.1(1.8)	^{A}29.5*(0.7)	^{B}32.5*(0.4)	^{A}29.3*(0.6)
Jun-Sep	^{A}20.5(0.8)	^{B}27.5(0.6)	^{A}20.9(0.8)	^{A}24.3(0.7)	^{B}33.4(0.5)	^{A}26.0(1.0)
Oct-Dec	^{AB}25.9*(0.7)	^{A}28.2*(0.6)	^{B}24.0*(1.6)	^{A}29.7*(0.8)	^{B}34.8*(0.4)	^{A}29.8*(0.2)
Fraction of FC	0-0.9 m			0-0.3 m		
20 Apr-May	^{A}0.92(0.00)	^{B}0.96(0.00)	^{AB}0.94(0.01)	^{A}0.90(0.01)	^{B}0.94(0.01)	^{A}0.89(0.02)
Jun-Sep	^{A}0.74(0.02)	^{B}0.97(0.01)	^{C}0.86(0.05)	^{A}0.74(0.01)	^{B}0.97(0.01)	^{A}0.79(0.05)
Oct-Dec	^{A}0.94(0.01)	^{B}1.00(0.01)	^{C}0.98(0.03)	^{A}0.90(0.01)	^{B}1.01(0.01)	^{A}0.91(0.03)

Gray et al. (2002) found that gaps with D/H of 0.2 and 1.0 resulted in the weakest gap effect on soil water storage whereas gaps with D/H of 0.4 and 0.6 generally showed a stronger gap effect (measured August - October during 5 years). The authors explain these results with a high amount of direct radiation in the northern part of the largest gaps, and with the proximity to edge trees in the case of the smallest gaps. In the northern edge of the gap in SUS_{NAT}, *SWC* tended to decrease from 2000 to 2001 relatively more than in the southern edge (Ritter et al. 2005a) which was explained by a high vegetation density. Lower SWC_{REL} in northern parts of the gap in SUS_{NAT} as compared to other gap positions was not found in either year (Dalsgaard 2007) thus high incoming radiation in the northern part of the gap did not influence the spatial variation in the soil water content. In the gap in RAV_{MAN}, SWC_{REL} in the upper 0.30 m was significantly lower ($p < 0.05$) in the northern part (0.93) of the gap than in the eastern part of the gap (1.00) in the summer 2001. This corresponds to the findings of Gray et al. (2002) and may be related to higher incoming radiation north of the gap centre (Ritter et al. 2005a). Further, SWC_{REL} in the upper 0.90 m was slightly higher (0.03) in the western part of the gap in RAV_{MAN} than the southern and northern parts during the fall and spring of 2001. These small effects cannot be readily explained, but they are unlikely to be caused by differences in the incoming radiation. Analyses in RAV_{MAN} were carried out as described for SUS_{NAT} (Dalsgaard 2007).

Gap effects on soil water storage, defined as the difference between closed forest and gap summer *SWC*, was higher in SUS_{NAT} (7.6-9.0 vol.%) than in RAV_{MAN} (7.0 vol.%) in 0-0.90 m depth, but lower in SUS_{NAT} (4.5-4.7 vol.%) than in RAV_{MAN} (9.1 vol.%) in 0-0.30 m soil depth. This may indicate that while the larger and more regular gap in RAV_{MAN} may have had a higher evaporation in the northern than in other parts of the gap, this did not result in weak gap effects on surface *SWC* (0-0.30 m) in general. Further, the central parts of the small and irregular gap in SUS_{NAT} may have been influenced by root water uptake in 0-0.30 m depth by released trees to a larger extend than the slightly larger and nearly circular gap in RAV_{MAN}.

7.3 Water fluxes in and near a small canopy gap

7.3.1 Intercepted water - throughfall and stemflow volumes

After removal of a deciduous forest canopy the rainfall intercepted by and evaporated from the canopy will decrease. However, the throughfall volumes of water reaching the ground in a small canopy gap will still be influenced by the surrounding canopy. Slavík (1957, in Geiger et al. 1995) found that growing season throughfall in the gap centre was 95-100% of *P*, whereas throughfall in the eastern edge of the gap was higher than *P* because of the prevalent westerly winds as well as the dripping of water from leaves on the edge trees (drippoints). In the present study, annual throughfall in gap and edge positions in SUS_{NAT} were 17 and 3% higher than for positions below the closed canopy (Dalsgaard 2007: *Table 1*). Annual throughfall as well as measurements in summer and spring were significantly higher in the gap than in the closed forest, but not in autumn or winter. In SUS_{NAT} in summer 2000 and 2001, positions in the gap received 19 (n=59 in total) or 30% (n=28 in total) more throughfall than positions below the closed canopy. Throughfall in edge positions was not significantly different from that below the closed forest canopy. Gap positions received approximately 100% (2000) and 90% (2001) of *P* (Dalsgaard 2007: *Figure 2*). In RAV_{MAN}, the gap received 29% higher throughfall in summer 2001 than positions below the canopy (Table 5) and the gap centre received approximately 105% of *P*. In RAV_{MAN}, gap and edge throughfall was not significantly different at any time and total as well as summer and spring throughfall were significantly different between gap and closed forest. Observed throughfall integrated over weekly to monthly measurements were linearly related to *P* as shown for RAV_{MAN} in Figure 5 and for SUS_{NAT} (Dalsgaard 2007: *Figure 2 and Figure 3*).

Table 5. *Periodic and total mean throughfall (mm) in Ravnsholte Forest. Different letters indicate significant differences ($p<0.05$) using a tukey-adjusted t-test. The standard error of the mean is shown in brackets. Methods as described in Dalsgaard (2007) and paper V.*

Time period	*Intact forest*	*Edge*	*Canopy opening*
July 3 – October 1 2001	297^{A} (9)	372^{1B} (42)	384^{B} (10)
October 1 – November 27 2001	90^{A} (2)	108^{B} (7)	107^{B} (4)
December 5 2001 – January 31 2002	169^{A} (4)	181^{A} (13)	184^{A} (5)
Total	555^{A} (13)	661^{B} (44)	676^{B} (17)

[1]One edge-observation was characterized as influential (*Cook's D* > 1). Without this observation the mean value was 334^{AB} (22) mm.

In both SUS_{NAT} and RAV_{MAN}, positions in the northern and eastern parts of the gaps tended to receive slightly more throughfall than western and southern parts, presumably due to the prevailing south-westerly winds (Pilegaard et al. 2003), but differences were not significant (Table 6). Relative to the highest observations found in the northern or eastern parts of the gap, the lowest observation was 87% in RAV_{MAN} and 89-93% in SUS_{NAT}. Across the whole measurement area (gap, edge and closed forest positions) in SUS_{NAT}, positions north of the gap centre received slightly more throughfall in autumn than other positions (Dalsgaard 2007), this was probably a combined effect of differences in canopy structure and wind direction.

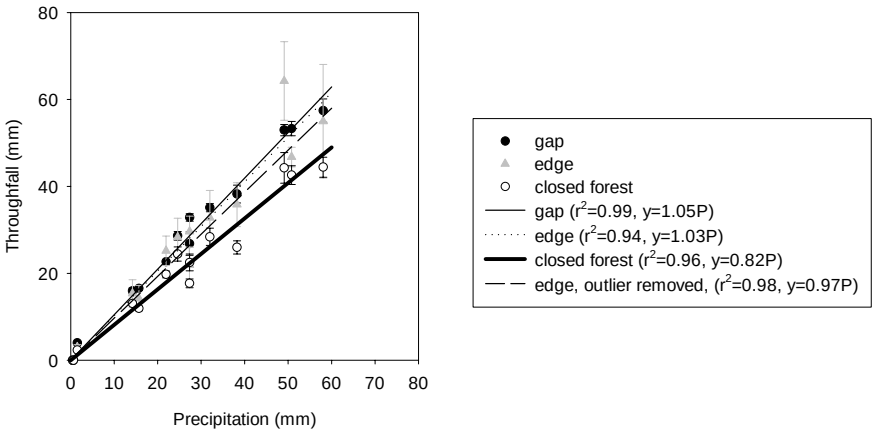

Figure 5. *Throughfall relative to precipitation in Ravnsholte Forest in gap, edge and closed forest when the canopy is in leaf. Error bars show ± one standard error of the mean.*

Table 6. *Periodic throughfall volume (mm) in two small canopy gaps. Positions are given relative to the centre of the opening. D/H-ratio was 2/3 in Suserup and 1 in Ravnsholte. The standard error of the mean is given in parentheses followed by the number of observations. No significant differences among positions (Tukey adjusted t-test, p<0.05). Methods described in Dalsgaard (2007) and paper V.*

	East	North	South	West
Ravnsholte June 2001 – January 2002	709 (8) 3	709 (24) 3	658 (33) 4	614 (51) 2
Suserup June 2000 – June 2001	633 (-) 1	629 (17) 3	585 (15) 3	586 (35) 3
Suserup June 2000 – January 2002	1242 (-) 1	1262 (37) 3	1167 (32) 3	1128 (62) 3

Stemflow at the edge of the gap was not measured in SUS_{NAT} or RAV_{MAN}, but stemflow from two exposed trees on a small ridge at the northern edge of a nearby gap in SUS_{NAT} was measured during a limited time period (Dalsgaard 2007). These results indicated that exposed crowns lead more water along the stems than trees in the closed forest (Figure 6, Dalsgaard 2007: *Figure 4*). These results are only indicative and do not show any direct gap effect due to a limited number of trees and exposures and the short duration of the measurements (only in winter). Neal et al. (1993) found that a possible edge effect of throughfall plus stemflow in European beech was confined to the outer 20 m of a forest edge.

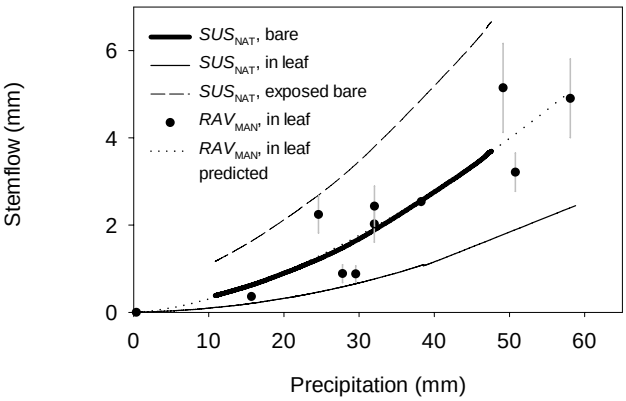

Figure 6. *Stand stemflow in Suserup Forest and Ravnsholte Forest. Data for Suserup Forest are from Dalsgaard (2007) and the predictions are based on regressions for European beech (r^2-values 0.67-0.76, basal area 22.5 $m^2 \cdot ha^{-1}$) and common ash (r^2-values 0.59-0.61, basal area 11.3 $m^2 \cdot ha^{-1}$). Error bars show ± one standard error of the mean. Predicted values for Ravnsholte are found as $y=0.0077x^{1.5984}$ (r^2-value 0.83) where y is stemflow(mm) and x is precipitation (mm).*

7.3.2 Tree transpiration and forest floor evapotranspiration

Transpiration in temperate forests is frequently limited by low soil water content (Granier et al. 2000a, b) and the high soil water availability at the edge of a small canopy gap is likely to result in a higher sap flow and transpiration in edge trees than trees in the closed forest during the progression of a growing season soil drought. Results from the present study showed that during the growing season 2000 in SUS_{NAT}, sap flow (average daily sum, average daily maximum) in subcanopy trees of European beech (tree height < 20 m) was lower for trees below the closed canopy than trees in the gap edge for most of the summer (after June) and significantly lower in September, where sap flow in subcanopy trees in the closed forest was 55% of sap flow in edge trees (paper III: *Table 3*). Among all trees in this study (trees in as well as below the dominating canopy) the daily maximum sap flow was significantly higher for trees near the gap than trees in the closed forest in August and September and the daily sums were significantly higher in September (paper III). See also *Figure 8* in Dalsgaard (2007), illustrating the increasing difference in sap flow between subcanopy trees in the edge

and closed forest during the growing season 2000. In early September 2000, *SWC* in 0-0.50 m soil depth below the closed canopy reached a minimum of 11 vol.%. After accounting for effects of *vpd* and radiation, regression analyses showed that sap flow in subcanopy trees below the closed canopy, as well as canopy trees, was significantly reduced (by 29-39%) in dry relative to in moist soil water conditions. Thus, trees were negatively affected by the progression of a seasonal soil drought. This was not observed for subcanopy trees in the gap edge (paper III: *Figure 8, Table 5*). Gap effects were not found for common ash. Tree transpiration for European beech calculated as total tree water use pr. area outlined by the crown periphery and expressed in mm (paper III: *Table 3*) decreased through the growing season for subcanopy trees beneath the canopy whereas subcanopy-trees in the edge of the gap sustained relatively high transpiration. However, these differences were not statistically significant. Estimates of tree transpiration may be subject to uncertainties in the calculation of whole-tree water use as well as in measurements of crown projection thus characterised by a larger error than measured sap flow. Possibly a larger sample size would have shown significant differences. Tree transpiration was estimated using the observed decrease in sap flow with increasing xylem depth (see Chapter 8.2.1). Tree sap flow and transpiration in edges of forest gaps has not been widely reported. It is reasonable to assume that trees take advantage of the new environmental conditions by root growth into the gap area (Müller and Wagner 2003), displacement of crowns toward spaces with light and an increase in the depth of the crown (Cienciala et al. 2002, Muth and Bazzaz 2002). The hydraulic system in branches acclimates and increases its ability to transport water in the xylem to sustain open stomata during hours with high light while decreasing the vulnerability to cavitation (Lemoine et al. 2002). Transpiration in a forest edge and in heavily thinned stands has been described. Relative to trees in the interior of the forest, trees in the north-facing edge had a higher transpiration and a deeper zone of xylem active in water transport (Cienciala et al. 2002). Differences were explained by stronger limitations to transpiration in the interior forest than in edges by soil frost in spring and by low soil water content in summer. In thinned stands, xylem sap flow (Vincke et al. 2005) and sap flow per unit leaf area was higher than in unthinned stands and the zone of active xylem was wider in thinned stands (Medhurst et al. 2002). The depth of the sap wood was not investigated in the present study, but the high sap flow in edge trees relative to trees below the dominating canopy agrees with the results referred to above.

Light received at the forest floor is considered to be the driving force for forest floor evapotranspiration (Baldocchi et al. 2000). It is therefore relevant to expect that forest floor evapotranspiration will increase after gap formation. In the present study and for SUS_{NAT}, it was found that forest floor evapotranspiration did not differ between gap and closed forest (Dalsgaard 2007: *Figure 7*). The daily soil + litter evaporation for three

days in August 2001 was 0.15-0.28 mm day^{-1}. For plots including low vegetation (small individuals of common ash regeneration) evapotranspiration was 0.7-0.9 mm day^{-1}.

7.3.3 Water budget

Gaps have a lower interception loss and transpiration than the closed forest and the resulting high soil water storage indicates that soil water drainage in small canopy gaps is larger than beneath a closed canopy. The contributions of each process to the water cycle in gaps may be predicted by using simulation models. Such studies are relatively few and many are in a monthly time resolution (Ritter and Vesterdal 2006, Ritter et al. 2005b, Vilhar et al. 2005). In the present study, annual and growing season drainage from the small canopy gaps in SUS_{NAT} and RAV_{MAN} was simulated in a daily resolution using the CoupModel (Jansson and Karlberg 2004, paper V). Details on parameter values and on the calibration including values of the normalized root mean square error (NRMSE; Schelde et al. 1998) are found in paper V (*Tables 2-7*) and *Figure 4* shows the simulated and observed soil water storage. From the model, annual drainage in gaps was estimated at 497-644 mm which is 76-104 % higher than beneath the closed forest. Zirlewagen and von Wilpert (2001) found, from daily simulations, that annual drainage was 65% higher in gaps than beneath the closed forest. In their study, several gaps were smaller than one tree crown presumably resulting in a slightly higher interception in these gaps relative to those in the present study, which may in turn influence the drainage flux. Simulation studies in mature European beech stands in gaps similar to those in the present study (D/H: 1-2/3) found that drainage (September or October 2001 to April 2003) was 24-37% larger than the drainage below the closed forest (Ritter et al. 2005b). They found either no significant differences in drainage due to gap size or a slightly higher drainage in the small gaps. From the present study, it was found that during the growing season, drainage was 231-390 mm in gaps and 80-128 mm in the closed forest (paper V: *Table 8*). These estimates seem high compared to those of Ritter and Vesterdal (2006) measuring in a mature European beech dominated stand. They found that in the gap (D/H: 2/3), drainage was 54 mm in the first growing season and 183 mm in the second growing season. In both years, they found no drainage beneath the closed canopy. Dormant season drainage in the present study was estimated at 64-66 mm higher for the gap (254-266 mm) than for the closed forest (188-202 mm) in SUS_{NAT}. In RAV_{MAN} it was similar for the gap (235 mm) and closed forest (234 mm). Ritter and Vesterdal (2006) found that for the first dormant period following gap formation, drainage from the gap was 179 mm relative to 50 mm in the closed forest while in the second dormant period closed forest and gap soil water drainage did not differ and were 170-190 mm. Ritter et al. (2005b) found that soil water drainage from gaps started two months earlier in the autumn than beneath the closed forest. In the

present study, the monthly fluxes, found from cumulating the daily fluxes, were never zero. In closed forest they were < 10 mm month^{-1} in August-December 2000 and in August-September 2001. In gaps they showed a minimum of 20-32 mm month^{-1} in June. Simulations in the present study for SUS_{NAT} and RAV_{MAN} showed that following gap formation, transpiration was reduced more than the interception loss (paper V: *Table 8*). A similar observation was made by Gray et al. (2002) who found that differences in soil water storage among different sized gaps and between closed forest and gap were primarily due to differences in evapotranspiration during periods without *P*. Compared to the two studies in European beech forest gaps (Ritter and Vesterdal 2006, Ritter et al. 2005b), the drainage fluxes simulated in the present study seem relatively high and with a large difference between gap and closed forest conditions in the growing season. That differences should be large in the growing seasons is reasonable as this is the time where differences in both transpiration and interception loss are large. The relatively high drainage fluxes estimated in the present study may be due to the higher time resolution (daily vs. monthly) and the specific model structure and the application of a specific gap microclimate characterised by low incident radiation. During the calibration of the CoupModel as presented in paper V, it was observed that the calibrated value for *LAI* in the gap edge simulations was low (≤ 50% of closed forest LAI) in the beginning of the growing season but increased (these are calibrated values) during the summer (paper V: *Table 6*). Further, a small measured decrease in gap SWC in late summer was not reproduced by the model (paper V: *Figure 4*). Both of these observations may be due to the lack of interactions between closed forest and edge, as well as between edge and gap water dynamics in the application of the one-dimensional model. Furthermore, it was observed that increasing gap *LAI* from 0.5-1.0 m^2 m^{-2} to values identical to the closed forest did not change the relationship between observed and simulated gap *SWC*. This indicates that gap evaporation was not determined to a large degree by the density of gap vegetation perhaps due to the relatively low radiation.

The importance of individual tree water use relative to the spatial variability of measured soil water storage was illustrated in SUS_{NAT}. Measured water use was the change in soil water storage at the measurement positions in and near the gap. Based on the measurements, estimated water use was found by parameterising a non-linear model originally developed for the description of fine root distribution depending on tree stem basal area and distance to trees (Nielsen and Mackenthun 1991, Dalsgaard 2007: *Eq. (1), Figure 6*). It was assumed that high water use is found where fine root density from trees is high. Evapotranspiration from soil, litter and low vegetation was not included in the model. This simple model explained 43% of the spatial variability in measured water use during selected periods in the summer 2000. Estimated growing season fine

root biomass was correlated to soil water potential in Norway spruce (*Picea abies* (L.) Karst.) (Ammer and Wagner 2002). The predictions of the simple model used in the present study show that in SUS_{NAT} only a few positions in this small gap, if any, were outside the influence of roots from the trees surrounding the gap. Based on the predictions (Dalsgaard 2007: *Figure 6*) the influence from canopy trees reached approximately 6-8 m from the stem of the tree. It was not possible to estimate the model with species specific parameters but there was a tendency that model residuals increased with the dominance of common ash. Species-specific patterns of soil water extraction have been demonstrated in a mixed stand of Norway spruce and European beech (Schume et al. 2003, 2004).

8 Canopy transpiration and stand water budgets

8.1 Mixing tree species, size and age

Forest management deals, among other things, with the decisions concerning stand manipulations in terms of both tree species, -age, and -size. Primarily based on what is profitable and what is possible - looking to existing natural or mixed uneven-aged managed forests for examples. These decisions may affect the hydrological cycle of forests. Dawson (1996) suggested a non-additive effect of mixing tree size on forest transpiration and water discharge caused by effects of hydraulic redistribution (passive root water transport from moist to dry soil layers) and deep rooting of large trees. Root growth in European beech was enhanced in mixed species stands compared to mono-specific stands for both coarse roots (Schmid and Kazda 2001) and fine roots (Leuschner et al. 2001) presumably influencing the amount of water available to this species. Schume et al. (2004) found non-additive effects of mixing species when investigating soil water depletion and recharge in mixed and mono-specific forests. It is not within the scope of this study to describe non-additive effects of mixing tree species, -size and -age on the water cycle. While such hypotheses are relevant, they cannot be tested here. Here, the focus is on the description of transpiration and water budgets in situations not included in studies of mono-specific even-aged stands as well as on comparing these to results in mono-specific European beech. Such data are necessary in order to document the possible effects on the water cycle of managing for structurally diverse forests. This chapter describes the transpiration and canopy conductance of two European beech canopies (stratified and non-stratified). The effect of tree height in a structurally heterogeneous stand is investigated based on the results in Schäfer et al. (2000) who found that the mean stomatal conductance was higher for small than for tall trees. To calculate transpiration from measurements of sap flow in European beech, the variation in xylem sap flow due to the xylem depth is investigated. Sap flow is presented for trees differing in size and species. Finally, results on stemflow, throughfall and simulated stand water budgets in a mixed and mono-specific stand are shown.

8.2 Transpiration and sap flow

8.2.1 Radial variation in sap flow

When measuring transpiration by the heat dissipation method, it is necessary to quantify the radial variation of the sap flow rate (i.e. Köstner et al. 1998). In the present study, sap flow in European beech trees in SUS_{NAT} decreased with increasing xylem depth

(paper III: *Figures 2 and 4*) as observed in other studies (Köstner et al. 1998, Granier et al. 2000a, Schäfer et al. 2000, Lüttschwager and Remus 2007). However, the observed decrease in sap flow was moderate compared to most other findings. Lang (1999) measured the radial variation in sap flow of a large open grown European beech tree and found a slight increase in sap flow rate with depth until a sapwood depth of 60 mm. Geβler et al. (2005) found sap flow to be similar for the outer 60 mm of xylem in 95-year-old European beech trees. Thus, the size of the tree crown and its exposure to the atmosphere may influence the radial variation in sap flow. Barbour and Whitehead (2003) found that wood density could explain variations in sap flow for open-grown trees of a conifer species. If differences in growth and stem increment among trees in the natural mixed forest (this study) induces differences in wood density this may add to the variability in the radial pattern of sap flow. Nadezhdina and Čermák (2003) found that the radial variation in sap flow reflected the structure of the root system with shallow roots supplying water predominately to the outer xylem and deep roots relatively more to the deep xylem. Thus, the moderate decrease in sap flow with increasing xylem depth observed in SUS_{NAT} may reflect that trees generally have deep roots compared to stands where steep sap flow profiles have been measured. The radial profiles changed diurnally with changes in *vpd* (paper III: *Figure 3*) but no common pattern for all sample trees emerged. Influence on the radial sap flow profile of changing *vpd* has also been observed by Granier et al. (2000a).

8.2.2 Sap flow variation due to canopy position and species

Trees beneath the main canopy of a closed stand receive less light than dominant trees. As a result, sap flow starts 1-2 hours later in the morning (Köstner et al. 1992) or have, during a day, up to 8 hours less time with significant sap flow rates (Martin et al. 1997). In the present study subcanopy trees of European beech in SUS_{NAT} were also observed to have a later onset of sap flow than dominant trees and an earlier decrease in the afternoon resulting in approximately 1-2 hours less time with sap flow during the day (illustrated in paper III: *Figure 7(a), June 21*). Diurnal transpiration of canopy trees was more closely correlated to *vpd* than subcanopy trees (height < 20 m) of European beech (paper IV) and correlation coefficients were 0.72-0.86 and 0.67-0.72, respectively. Maximum and mean sap flow rates did not vary systematically with tree size in SUS_{NAT} (paper III: *Figure 6*) which was also found in studies of heterogeneous coniferous stands (Simpson 2000, Barbour and Whitehead 2003). Granier et al. (2000a) found that in a 30 year old stand of European beech, sap flow rates increased with stem diameter (stem diameter approximately 6-20 cm). Calculated tree water use and tree water use related to the crown projected area often increase with tree size (Köstner et al. 1992, Martin et al. 1997, Simpson 2000). In the present study, tree transpiration pr. crown

projection area (expressed in mm) for European beech in SUS_{NAT} (paper III: *Figure 6*) tended to increase with stem diameter and tree height but not significantly (the increase with tree height was near-significant, p=0.06). By examining *Figure 8* (paper III) there is a tendency that sap flow (daily sum of J_s) of suppressed subcanopy trees was slightly more limited due to low soil water content during a progressive soil drought than canopy trees. From regression analyses it was found that in dry soil conditions, sap flow in suppressed subcanopy trees was 62-64% and in canopy trees 61-71% of sap flow in moist soil conditions (paper III: *Table 5*). However, the monthly mean values of sap flow (paper III: *Table 3*) were not significantly different. The monthly mean values of transpiration (paper III: *Table 3*) were lower for suppressed subcanopy trees in the closed forest than for canopy trees during July and August supporting the observation that they experienced a slightly higher limitation in sap flow than canopy trees. This could be a result of a shallower root system for small than for large trees (Dawson 1996, Zimmermann et al. 2000). A higher sensitivity of stem basal area increment to water deficit of suppressed than dominant trees of European beech was found by Piutti and Cescatti (1997).

In this study, it was found that sap flow rates (monthly mean of the daily sum and maximum of J_s) of common ash were significantly lower than those of European beech (paper III: *Table 4*). Unfortunately, sap flow measurements for common ash could not be scaled to tree and subsequently stand transpiration because of uncertainty in the xylem depth. Steep gradients in J_s along the length of the sap flow probe including the presence of inactive sap wood may result in an underestimation of integrated J_s (Clearwater et al. 1999). If measured sap flow (paper III) in common ash is corrected as suggested in Clearwater et al. (1999) assuming that xylem depth was 10 mm (Ladefoged 1952, Cochard et al. 1997, Hölscher et al. 2005), sap flow rates would increase (Figure 7A). If such a correction is realistic, differences in J_s between European beech and common ash in paper III would decrease but whole tree transpiration would still be low in common ash relative to European beech (Figure 7B). For the sample tree on June 19, 2000 in Figure 7B, European beech transpiration was 68.5 kg day^{-1} and the corrected common ash transpiration would be 18.1 kg day^{-1}, 26% of European beech. This difference emerges due to differences in sap wood area.

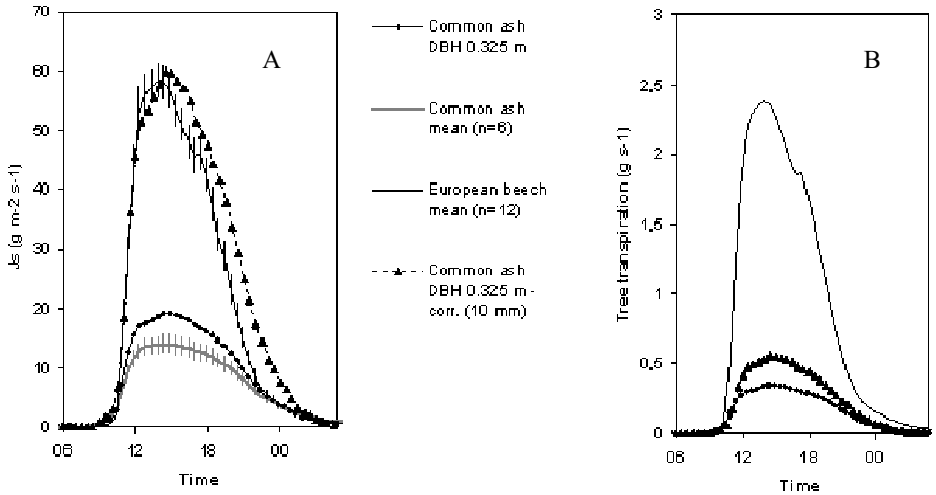

Figure 7. A: *Mean sap flow for common ash and European beech measured in Suserup Forest on June 19, 2000. Highest observed individual tree sap flow for common ash as well as corrected sap flow for this tree according to Clearwater et al. (1999) is also shown. Error bars show ± one standard error of the mean. DBH is stem diameter at breast height (1.3 m).* B: *Sap flow scaled to whole tree transpiration (g water s^{-1} $tree^{-1}$) for an example tree of 0.305 m below-bark stem diameter: i) European beech (based on mean sap flow), ii) observed common ash, and iii) corrected common ash.*

Corrected J_s as suggested by Clearwater et al. (1999) increases non-linearly with observed J_s. By using the common ash tree with the highest observed J_s, Figure 7 illustrates that the maximum corrected J_s for common ash would approach the level observed for the mean J_s of European beech. Hölscher et al. (2005) found that mature trees of common ash had very low sap flow rates compared to European beech and three additional diffuse porous species in part explained by a low leaf area. In the same study, common ash did not appear to respond to soil water depletion and changes in *vpd* in contrast to European beech. Stöhr and Lösch (2004) found that saplings (stem diameter 1-3 cm) of common ash had very high sap flow rates similar to rates measured in lianas and tropical trees. Stöhr and Lösch (2004) did not use the heat dissipation technique. Ladefoged (1963) found that transpiration rates for common ash were slightly higher than for European beech. For common ash, published results seem to be contradictory. For other ring porous species, it has been found that sap flow and transpiration is low compared to diffuse porous species (Oren and Pataki 2001, Wullschleger et al. 2001). Differences in leaf area between European beech and common ash may explain differences in sap flow rates, however, this was not measured in the present study.

8.2.3 Transpiration and canopy conductance in European beech canopies

In this study, a method similar to that described by Schäfer et al. (2000) was used to test the hypothesis that mean tree stomatal conductance (g_s) decreased with height in European beech in SUS_{NAT} (paper IV). g_s was calculated from sap flow measurements (paper IV: *Eq. (3)*) using an estimated tree leaf area calculated from measured crown dimensions and a three-dimensional crown model (Brunner 1998). Estimated tree leaf area agreed well with predictions from a regression model (LA_{reg}) based on destructive measurements in European beech (Schäfer et al. 2000) (estimated tree leaf area = 1.099 $\cdot$ LA_{reg}, r^2 -value = 0.83). In this study, g_s represents the total conductance (stomatal and boundary-layer). A reference g_s was calculated based on Oren et al. (1999b) (paper IV: *Eq. (4)*) and related to tree height in the range 14-29 m. The hypothesis concerning the effects of tree height on reference g_s was not supported by the results in paper IV. Though tall trees generally showed low reference g_s, the variability among small trees was very large and a significant relationship between the reference g_s and tree height did not emerge (paper IV: *Figure 5*). Only sap flow data obtained in periods with high soil water availability were used.

Further, it was tested if the sensitivity of the boundary line (potential) canopy conductace (g_c) to changes in *vpd* for European beech differed between SOR_{MAN} (height 25 m) and SUS_{NAT} (tree height 14-29 m). A high sensitivity to *vpd* is commonly observed to coincide with a high reference stomatal conductance (Oren et al. 1999b, Oren and Pataki 2001). To avoid differences between the two sites that could be due to root distribution or soil characteristics, the analyses were done using data from periods with high soil water availability. g_c was calculated by inverting the Penman-Monteith equation (paper IV: *Eq. (1), (2)*) and subject to a boundary-line selection similar to that used in Schäfer et al. (2000) to identify data representing the upper boundary g_c. The upper boundary g_c in the two stands was represented by a model incorporating *vpd* (Oren et al. 1999b, paper IV: *Eq. (4)*). Because of the unknown leaf area of European beech in SUS_{NAT}, estimates of g_c were standardized according to Weisberg (1985) (see paper IV). Both g_c and standardized g_c were similar in the two stands (paper IV: *Figure 4*) and the sensitivity to *vpd* represented by a parameter (m) (paper IV: *Eq. (4)*) did not differ between sites. In the preliminary analyses of these data (not shown), it was found that calculated g_c displayed expected patterns and increased with increasing *PAR* and saturated at high levels of *PAR* . Further, g_c showed a hyperbolic decrease with increasing *vpd* like observed for a European beech canopy by e.g. Herbst (1995).

Transpiration May 5-September 30 2000 was 203 mm in SOR_{MAN}. This is slightly lower than transpiration in three European beech stands presented by Granier et al. (2003),

218-333 mm. In addition to the relatively cool summer of 2000, these differences may be explained by larger *LAI* in these three stands (approximately 6 m^2 m^{-2}). Granier et al. (2000b) found that leaf area was an important structural determinant for transpiration and canopy conductance. Transpiration from SUS_{NAT} (paper IV) was 114 mm measured June 15 - September 30 and including only the contribution from European beech. As measurements started on June 15, comparisons with integrated growing season transpiration are not relevant. For the period June 15 - September 30, European beech transpiration in SUS_{NAT} was approximately 80% of transpiration in SOR_{MAN}. For both SUS_{NAT} and SOR_{MAN}, transpiration was closely related to *vpd* and global radiation (paper IV: *Figure 1*). In paper IV, it was observed that diurnal canopy-scale transpiration for European beech in SUS_{NAT} and SOR_{MAN} was near a 1:1 relation at high transpiration rates, whereas at intermediate rates, SUS_{NAT} had a transpiration of approximately 80% of SOR_{MAN} (paper IV: *Figure 2*). In the present study (paper IV), it was found that diurnal transpiration in SOR_{MAN} was slightly closer related to *vpd* than to *PAR* (correlation coefficients 0.96 and 0.80) whereas in SUS_{NAT}, diurnal transpiration was closer related to *PAR* than to *vpd* (correlation coefficents 0.91 and 0.84).

8.3 Interception loss, throughfall and stemflow volumes

Interception varies with the storage capacity of leaves, stems and branches in the canopy and shrub layer as well as in forest floor litter. Other influencing variables are the angle of branches and leaves and meteorological variables like the amount, intensity and duration of rainfall, wind speed, air temperature and air humidity (Crockford and Richardson 2000, Levia and Frost 2003). Thus, results tend to be variable and generalizations among similar forest types is difficult to establish (Crockford and Richardson 2000). However, due to the seasonality of their leaf coverage and possible seasonality in rainfall and meteorological patterns, temperate deciduous forest interception loss tends to be lower (9-40% of *P*, Thomsen et al. 2003, review in Ladekarl 2001) than in coniferous forests where the interception loss is often near 50% of *P* (e.g. Thomsen et al. 2003).

In this study (Dalsgaard 2007), throughfall was 74.3% of *P*, based on the regression of throughfall vs. *P*, and stemflow was 2.2% of *P* in the growing season in SUS_{NAT}. In RAV_{MAN}, throughfall was 82% and stemflow 6.7% of *P* in the growing season (this study, Chapter 7.3.1). On average and for the growing season in European beech, Granier et al. (2000a) found that throughfall and stemflow was 74% and 5% of *P*, respectively, and Aussenac and Boulangeat (1980) found throughfall and stemflow in European beech to be 76% and 3% of *P*, respectively. In the comparison above, a higher *LAI* (5.6-5.7 m^2 m^{-2}) measured by Granier et al. (2000a) may explain the slightly higher

interception loss relative to results in RAV_{MAN}. Further, the lower percentage of stemflow relative to *P* in SUS_{NAT} than in the pure European beech stands may be caused by the presence of common ash (Dalsgaard 2007: *Figure 4*), as well as old and scarred individuals in SUS_{NAT} with a larger storage capacity on the bark and stem surfaces than young trees (Levia and Frost 2003). Pilegaard et al. (2003) found growing season interception loss to be 36% of *P* in pure European beech, which is higher than all of the above results. For the dormant season, it was found in the present study (Dalsgaard 2007) that throughfall was 80% and stemflow 6.0% of *P* in SUS_{NAT}. For pure European beech, Aussenac and Boulangeat (1980) found throughfall and stemflow to be 85% and 9% and Pilegaard et al. (2003) found an interception loss of 9% of *P*.

Deguchi et al. (2006) found in a 12 m tall Japanese temperate deciduous forest (maximum *LAI* 4 m^2 m^{-2}) that growing season and dormant season interception loss were relatively similar, namely 17.6 and 14.3% of *P*, respectively. This illustrates that seasonal variation in structure may not infer a comparatively large seasonal variation in interception loss.

8.4 Stand water budgets

The CoupModel (paper V) was calibrated using measured soil water storage April-August 2001 at both sites. Measured *SWC* was available in SUS_{NAT} for approximately 18 months and in RAV_{MAN} for approximately 7 months. Simulations were made for two years and one year at the two sites, respectively. The normalized root mean square error NRMSE was used to evaluate the simulations, where a value of 0 indicates a perfect match between simulated and observed soil water storage. In RAV_{MAN}, values of NRMSE were 0.04-0.12 for the calibration period April to August 2001 indicating good model representation. In SUS_{NAT}, values of NRMSE for the calibration period April to August 2001 were 0.04-0.14 in the three deepest soil layers and 0.23 in the upper 14 cm. In SUS_{NAT} the values of NRMSE for the period April to August 2000 which were not used for calibration were 0.05-0.17 for the three deepest soil layers. Further details on the comparison between measured and simulated soil water storage are found in paper V (*Table 5 and Table 7*).

The simulated stand water balances in this study represent years and sites with an annual *P* (corrected) of 766-873 mm and a growing season *P* of 373-551 mm (paper V: *Table 8*). Annual evapotranspiration was 502-519 mm, less than the 581 mm found by Christiansen et al. (2006) in a 26 year old pure stand of European beech (*LAI* 4.5 m^2m^{-2}) and slightly higher than the 490 mm (mean of 1992-1999; range 381-594 mm) found by Ladekarl et al. (2005) in sessile oak (*Quercus petraea* L.) in Denmark. Simulated

annual drainage (paper V) was 282-319 mm, similar to results in Christiansen et al. (2006) and slightly lower than the 390 mm found on average by Ladekarl et al. (2005; range was 197-536 mm). *P* for these two studies was 853 mm and 880 mm (mean; range was 578-1029 mm). In May to October evapotranspiration (paper V) was 414-419 mm, lower than the 486 mm presented in Davi et al. (2005) for a 30 year old stand of pure European beech (*LAI* 6 m^2m^{-2}). A lower evapotranspiration in the mature European beech stand and the natural forest in this study than in the two young European beech stands (Davi et al. 2005, Christiansen et al. 2006) may partly be explained by differences in *LAI* in addition to differences in meteorological conditions. In the mixed stand, the late leaf development of common ash and pedunculate oak resulted in relatively low *LAI* in early summer. Also, differences in the models used may have influenced the estimates. Simulated annual soil water drainage was related to annual *P* for different land uses in Denmark (Bastrup-Birk and Gundersen 2004) and drainage estimates in this study (paper V) were placed in the emerging relationship on line with results from old stands of sessile oak. The distribution of annual evapotranspiration to interception loss, canopy transpiration and forest floor evaporation was 27%, 58% and 15%, respectively, in a young stand of European beech (Christiansen et al. 2006). In the two stands in this study (paper V), the distribution to interception loss, canopy transpiration and forest floor evaporation was 23-29%, 42-48% and 28-31%, respectively, indicating a lower contribution from transpiration and a higher contribution from forest floor evaporation. For the period May-October, Davi et al. (2005) found a contribution to evapotranspiration of 23%, 65% and 12% from interception loss, canopy transpiration and forest floor evaporation, respectively. Estimates from paper V from May to October were 25-31%, 52-57% and 17-18%. From the simulated water budgets in SUS_{NAT} and RAV_{MAN}, (paper V: *Table 8 and Table 9*) it was found that interception loss was higher in SUS_{NAT} (120-129, May-October and 140-144 mm annually) than in RAV_{MAN} (104 mm, May to October and 117 mm annually). In contrast, annual transpiration was higher in RAV_{MAN} (241 mm) than in SUS_{NAT} (219-220 mm). This is consistent with a higher calibrated maximum stomatal conductance in RAV_{MAN} than in SUS_{NAT} (paper V: *Table 2*).

9 Discussion: European beech forest structure and the water cycle

Chapter 5 introduced the hypotheses addressed in this study. Those concerning the canopy gap and those concerning stand scale processes are each considered in turn. Following this, some methodological considerations regarding the empirical and simulation studies are given.

9.1 Discussion of hypotheses: water cycle in small canopy gaps

> A1-A5: It was hypothesized that relative to beneath or in the closed forest, the formation of a small canopy gap ($D/H \leq 1$) in mature European beech dominated forests leads to increasing: i) soil water storage, ii) throughfall, iii) forest floor evapotranspiration, iv) edge tree transpiration and sap flow, and v) soil water drainage.

High soil water storage in the gaps relative to positions in the closed forest was clearly demonstrated primarily for summer and autumn. Soil water storage decreased during the growing season, also in the gap as shown in Dalsgaard 2007 (*Figure 5*), but significant differences between closed forest and gap persisted. While in summer, gap *SWC* was ≥ 90% of field capacity, positions in the closed forest had *SWC* of 64-74% of field capacity in 0-0.90 m soil depth based on seasonal averages. High growing season soil water storage in small gaps has been observed in several studies (i.e. Bauhus and Bartsch 1995, Ritter et al. 2005b, Gray et al. 2002). *SWC* in gap edges was generally intermediate between closed forest and gap positions. Based on the *SWC* relative to field capacity, edge positions were significantly different from forest positions in the first growing season after gap formation, except for RAV_{MAN} in 0-0.30 m depth where edge and closed forest positions were similar. For RAV_{MAN}, this could indicate that roots of edge trees have a high density in 0-0.30 m soil depth, but a relatively low density in 0.30-0.90 m depth. In the second growing season, edge and closed forest *SWC* relative to field capacity were similar.

Throughfall volumes were significantly higher in canopy gaps than below the closed forest during spring and summer in SUS_{NAT} and in summer and fall in $RAV_{MAN,}$ leading to significant differences annually and for the entire measurement period. These results are supported by observations by Zirlewagen and von Wilpert (2001). In contrast, Ritter and Vesterdal (2006) found no differences in gap and closed forest throughfall in neither dormant nor growing season. Their measurements were possibly influenced by

vegetation overtopping the funnels in the gap which could have caused the lack of significant differences. In RAV_{MAN}, edge positions received the same amount of throughfall as gap positions, whereas in SUS_{NAT}, edge positions received the same amount as in the closed forest.

Neither evaporation nor evapotranspiration from the forest floor (soil, litter and low vegetation) differed between gap and closed forest in SUS_{NAT} based on the limited amount of observations in August 2001. Evaporation was within the range observed by Wilson et al. (2000). The lack of difference was contrary to expectations as the available energy at the forest floor is regarded as an important driving factor for evaporation in dry conditions (Baldocchi et al. 2000). Forest floor evaporation rates in an undisturbed *Nothofagus* forest were up to 0.5 mm day^{-1} and closely coupled to *vpd* through gusts originating from above the tree canopy (Kelliher et al. 1992). Wilson et al. (2000) found that the annual fluctuations in forest floor evaporation were more closely related to *vpd* and litter water content than available energy. A close coupling of evapotranspiration to *vpd* in the air above the canopy may partly explain the lack of differences found in the present study between closed forest and gap positions. The time of the growing season (late August 2001) and possible lack of direct light in the gap may also be part of the explanation.

Measurements of sap flow rates showed that trees near the gap benefited from the high availability of soil water during soil drought in the growing season. The results show that the release of saplings and subcanopy trees after the formation of a small canopy gap in a temperate deciduous forest may rely on soil water effects as well as on effects of increased radiation. Branch hydraulic architecture in recently thinned trees acclimates to increased levels of light by developing a higher hydraulic conductivity and xylem safety relative to cavitation (Lemoine et al. 2002). This reduces any hydraulic limitations to carbon assimilation (Maherali et al. 1997). It is therefore likely that when subcanopy trees are released following gap formation they are able to take advantage of the increase in light interception because of high soil water availability. This possibly results in a high growth rate for trees at the edge of canopy gaps (Catovsky et al. 2002) and contributes to the crown expansion observed in edge trees (Hibbs 1982, Muth and Bazzaz 2002). Factors affecting the availability of soil water in canopy gaps, i.e. the water holding capacity of the soil (Vilhar et al. 2005), soil hydraulic conductivity (Čermák and Prax 2001) and competition from herb or shrub vegetation (McGuire et al. 2001), may influence tree growth and thus long term gap development.

As expected, simulated soil water drainage was higher from positions in the gap than in the closed forest. Differences were most distinct in the growing season. This was also

observed by Zirlewagen and von Wilpert (2001), Ritter et al. (2005b) and Ritter and Vesterdal (2006), though, for the two latter references, the differences between closed forest and gap soil water drainage seemed low compared to those observed in this study. Vilhar et al. (2005) found that differences between canopy gap and closed forest were not clear due to variable microsites and dry conditions during the measurement period. The daily time resolution in the present study may have magnified differences in drainage between closed forest and gap positions relative to simulations with a monthly resolution. Further, using a specific microclimate for the gap conditions characterized by low radiation could also have influenced results. During the calibration of the CoupModel, it was found that simulated water storage in the gaps was insensitive to changes in the leaf area of gap vegetation indicating that the evaporative demand was low in these gaps despite a significant increase in light relative to beneath the closed forest. The CoupModel was not able to accurately reproduce the slightly decreasing gap soil water content in summer presumably due to its one-dimensional structure and lack of interaction among the closed forest, edge and gap situations. This is probably part of the reason why estimates of gap soil water drainage are relatively high in the present study. The application of the CoupModel and possible improvements are also discussed in Chapter 9.2 and 9.3.

Overall, the expected effects of gap formation on soil water storage, throughfall and soil water drainage were observed. Higher tree transpiration in the gap edge was not statistically confirmed but higher sap flow rates were confirmed supporting the hypothesis concerning the effect on edge trees of high water availability. The similarity in forest floor evapotranspiration between closed forest and gap was contrary to expectations.

> A6-A8: It was further hypothesized that spatial effects in the gap would emerge in the spatial pattern of soil water storage and throughfall owing to the pattern of incoming radiation, prevailing wind direction and the position and size of trees.

The northern part of the gap in RAV_{MAN} showed significantly lower *SWC* relative to field capacity in summer than the eastern part of the gap which could be due to higher incoming radiation. This was not observed for SUS_{NAT}. Though not statistically significant, the difference in throughfall between the relatively high values in the northern and eastern parts of the gaps and those in the southern and western parts was slightly higher in RAV_{MAN} than in SUS_{NAT}. The hypothesized spatial patterns in soil water storage and throughfall were not very clear. They were, however, slightly more visible in the artificially established gap in the managed forest than in the naturally established and slightly smaller gap. This may have been due to both the difference in

gap size and in gap edge regularity. Irregular gap edges and saplings present in the gap influence soil water dynamics. Further, as noted by Gray et al. (2002), dead standing trees may cast shade and gap development following the slowly decreasing vitality of the gap-maker may obscure the spatial patterns in microclimate potentially observed caused by the influence of i.e. solar elevation and wind direction.

A simple model including the distance to trees and their basal area was able to explain 43% of the variability in measured water use across the measurement area in SUS_{NAT} (Dalsgaard 2007). The model may be a first step to link root water uptake to individual tree position and the structure of a gap edge. Improvements could incorporate the distribution of resources (Leuschner et al. 2001) in addition to the distribution of trees. Predictions from the simple model demonstrate that the influence of water uptake by large canopy trees reaches approximately 6-8 m from the tree stems indicating that in the gap in SUS_{NAT}, the majority of the gap area will, to some degree, be influenced by water uptake of the edge trees. The model was estimated assuming that drainage and forest floor evapotranspiration was negligible. Future development of the model should consider both processes.

The expected patterns in *SWC* and thoughfall due to wind direction and solar radiation in the northern part of the gap were not confirmed (thoughfall) or very weak (*SWC*) in the gaps studied. As expected, the water dynamics in and near the gap was related to tree size and position.

The gap case studies presented here were followed for only one and two years and the time of gap closure, i.e. the reversal of the hydrological conditions in the gap to the conditions found in the closed forest, cannot be estimated. The observation from SUS_{NAT} that soil water storage in the gap edge was similar to positions in the closed forest in the second year after gap formation indicates that gap closure relative to the hydrological cycle is rather fast. The high water use of trees in the gap edge observed from both sap flow measurements and simulated root water uptake and illustrated graphically in the SUS_{NAT} gap in the summer 2000 tend to support this. Throughfall in gap positions decreased from 99 to 89% of P from the first to the second summer, but in the closed forest throughfall also decreased thus these changes may not be related to gap closure. No decrease from the first to the second year was observed in the simulated drainage from gap positions relative to closed forest positions. Gray et al. (2002) show that gaps may reverse to the pre-gap conditions of soil water storage after approximately 6 years and Ritter et al. (2005a) showed that radiation in the gap had decreased from the first to the second year after gap formation in the natural forest.

Gaps are formed as a result of tree mortality and used as a tool in the management of forests. Thus, effects of gap formation on the hydrological cycle in forests is a relevant object of investigation. Some processes do not work on the gap scale, i.e. stemflow as well as throughfall volumes from drippoints are considered to be point sources (Ladekarl et al. 2001). Soil variability and the nature and amount of woody debris (Heinemann et al. 2000, Gray et al. 2002) may influence the microclimate and local hydrological balance. These other scales and structures overlaying the structure of the forest canopy must also be included in hydrological studies when relevant.

9.2 Discussion of hypotheses: stand scale processes in the water cycle

> B1: It was hypothesized that the mean stomatal conductance decreases with increasing tree height in European beech and that differences in the distribution of European beech tree height in the two stands leads to differences in the sensitivity to *vpd* in European beech canopy conductance.

Among the individual European beech trees in SUS_{NAT}, tall trees generally showed low mean stomatal conductance (g_s), but the variability among small trees was very large and a significant relationship between the reference g_s and tree height did not emerge. This may have been due to recently changed microclimatic conditions for many of the small trees due to the formation of a canopy gap possibly inducing tree level acclimation of the conducting system (Lemoine et al. 2002). However, a direct relationship between tree social position or crown exposure and the calculated reference g_s could not be established. For canopy conductance (g_c) of European beech, observations from the two sites were very similar and the sensitivity of changes in *vpd* did not differ between stands. The stated hypothesis was not supported by the results in paper IV and the overall result is that, in this study, tree height or height distribution does not affect European beech transpiration or g_c. A similar conclusion was drawn by Granier et al. (2000a) who found that a model of g_c incorporating effects of *vpd*, global radiation, air temperature and soil water deficit provided equally good estimates for two European beech stands differing in height and age. Köstner (2001) found that maximum transpiration relative to stand *LAI* decreased with age in Norway spruce but was constant in European beech. In a number of studies, tree height has been found to influence tree transpiration through a comparatively low stomatal and hydraulic conductance in tall trees (e.g. Schäfer et al. 2000 (European beech), Ryan et al. 2000 (*Pinus ponderosa* Laws.), Delzon et al. 2004 (*P. pinaster* Ait.), Addington et al. 2006 (*P. palustris* Mill.)). Such an influence is thought to be related to the observed decrease in height and biomass growth as stands grow taller (e.g. Ryan et al. 2006). However, though limitations to gas exchange have been observed due to increased height, it is not

a universal finding (e.g. Phillips et al. 2002, Ewers et al. 2005). Any effect of tree height on the conducting system may be mitigated by a decrease in leaf area:sapwood area - ratio, a reduced minimum leaf water potential, an increase in sapwood conductivity or in an increase in stem capacitance (Ryan et al. 2006).

It was observed that while the daily as well as the intermediate diurnal rates of transpiration in SUS_{NAT} were approximately 80% of those in SOR_{MAN}, the relationship approached unity at high diurnal transpiration rates. This was interpreted as a higher resistance to transpiration in the soil-plant-atmosphere pathway in SOR_{MAN} than in SUS_{NAT}. In the present study, measurements did not allow for an identification of possible resistances to transpiration in the hydraulic pathway from the soil to the leaf. Observations indicated that *vpd* is slightly more important in the regulation of transpiration in SOR_{MAN} than in SUS_{NAT}. The position of the *vpd* measurements relative to the canopy surface (in SOR_{MAN} at the canopy surface, in SUS_{NAT} 2 m above the ground) may result in a closer relationship in SOR_{MAN} than in SUS_{NAT}. However, the close correlation to *vpd* in SOR_{MAN} may also be related to the importance of the imposed evaporation rate (Jarvis and McNaughton 1986) prompting some stomatal closure (Hogg and Hurdle 1997, Meinzer et al. 1997). The close correlation of transpiration to *vpd* in both SUS_{NAT} and SOR_{MAN} indicates that both canopies were closely coupled to the surrounding atmosphere. Jarvis and McNaughton (1986) defined the decoupling coefficient Ω as an index (value 0-1) of the degree of stomatal control of transpiration and the relative importance of radiation and *vpd* on transpiration. When Ω is near 0, the stomatal control of transpiration and the influence of *vpd* dominates over the influence of radiation. In European beech canopies, Ω was 0.05-0.2 (Herbst 1995, Granier et al. 2000a) and 0.28 (Magnani et al. 1998), indicating relatively close coupling. For red maple (*Acer rubrum* L.), transpiration of mature trees were closer coupled to the air than subcanopy trees (Wullschleger et al. 1998, 2000), which supports the observations in the present study that canopy trees were closer correlated to *vpd* than trees beneath the canopy. If the European beech canopy in SOR_{MAN} experiences a higher limitation of transpiration than the canopy in SUS_{NAT} due to a high imposed *vpd*, the results observed for the relatively cool growing season in 2000 may not be fully representative of warm summer periods.

> B2: It was further hypothesized that the process-based water balance simulation model CoupModel (Jansson and Karlberg 2004) adequately represents the processes in the water cycle in European beech dominated mature forests as evaluated from comparisons of the predicted and observed soil water storage. Due to the dominance of European beech in both stands (natural and managed), it was expected that the simulated transpiration (governed by the calibrated value

for the mean stomatal conductance) and interception loss (calibrated to measured stemflow and throughfall volumes) would be the same.

Soil water storage was well predicted by the model. Best agreement between simulated and observed values was found for the growing season whereas some overestimation of soil water storage was found in the dormant season. Transpiration relative to *LAI* and the calibrated value of the maximum stomatal conductance was lower in the natural than in the managed stand. Due to the presence of common ash and pedunculate oak, it is natural to ascribe these differences, at least partly, to the effect of the species composition. Common ash and pedunculate oak are both ring porous species. Later leaf development in spring and earlier leaf shedding in fall have been observed for ring porous compared to diffuse porous species (Oren and Pataki 2001, Thomsen unpubl. data) resulting in less days with a potentially high transpiration. In contrast to diffuse porous species, ring porous species are often subject to embolization following the first frost episodes in autumn (Cochard et al. 1997, 2001). Further, in spring, many ring porous species depend fully on the development of new xylem while many diffuse porous species may be able to rely on existing sap wood during leaf development (Cruiziat et al. 2002). Sap flow rates for common ash were low relative to European beech (Hölcher et al. 2005, paper III and Figure 7 in Chapter 8.2.2). Sap flow rates for European beech were high compared to those of other diffuse porous species like *A. pseudoplatanus* L., *Carpinus betulus* L. and *Tilia cordata* Scop. (Hölscher et al. 2005). Transpiration was high in European beech compared to Norway spruce (Schume et al. 2003, 2004), but lower and characterized by a stronger stomatal control than in *Alnus glutinosa* ((L.) Gaertn.) (Herbst et al. 1999). Oren and Pataki (2001) conclude that diffuse porous species in their study had a higher g_s and a higher sensitivity to increasing *vpd* than did ring porous species, resulting in a higher potential transpiration in stands dominated by diffuse porous trees. Stand transpiration was dominated by water use of diffuse porous species in a mixed deciduous forest in USA (Wullschleger et al. 2001).

It was concluded from paper IV that tree height or height distribution did not affect transpiration. Sap flow measurements represented individuals with stem diameter ≤ 0.7 m. Sap flow of the largest European beech tree in SUS_{NAT} (stem diameter=0.7 m) was very low during late summer 2000 (data not shown) and possibly the trees selected for sap flow measurements did not represent the very large and presumably old individuals in the stand. No effect of age on stand transpiration was observed up to an age of 125 years (Köstner 2001), but in SUS_{NAT} European beech trees can be more than double this age. A decline in sapwood area and subsequently transpiration was found for *Eucaluptus sieberi* (L.) Johnson with stand age up to 160 years (Roberts et al. 2001).

Vertessy et al. (2001) found a decrease in transpiration with age up to 240 years in *Eucalyptus regnans* F. Muell. Delzon and Loustau (2005) found a decrease in transpiration in *Pinus pinaster* Ait. up to an age of 91 years . In pedunculate oak of low vitality, Vincke et al. (2005) found low sap flow rates and low transpiration. Thus, while differences in the species composition in the two stands observed in this study may be the reason or part of the reason for the relatively modest differences in simulated transpiration, age or vitality cannot be ruled out and future investigations should try to uncover such effects.

Simulated interception loss was higher in SUS_{NAT} than in RAV_{MAN}, both annually and for the growing season. The difference may be related to a higher *LAI* in SUS_{NAT} (in parts of the growing season) and a relatively low stemflow in common ash while stemflow in RAV_{MAN} was slightly higher. The structure of the forest influences the turbulent mixing of air at the top of the canopy (Monteith and Unsworth 1990) which in turn influences the rates of evaporation (McNaughton and Jarvis 1983, Deguchi et al. 2006). The roughness of the canopy was slightly higher in a natural deciduous forests than in an even-aged European beech stand expressed in a measured roughness length relative to stand height of 0.08 and 0.06 respectively (Dellwik and Jensen 2000, Knohl et al. 2003). If the two stands used in the present study differed in roughness, the throughfall and stemflow measurements used in the model calibration may have been influenced by high turbulent mixing and higher evaporation rates, resulting in differences in the predicted interception loss.

Based on the comparison of measured and simulated soil water storage it is concluded that the CoupModel provided a good representation of forest water balance of the sites studied. The observed, but moderate differences between stands in simulated interception loss and transpiration as well as in the calibrated values for the maximum stomatal conductance were not expected. From the CoupModel simulations, it was observed that simulated forest floor evaporation was high compared to other simulation studies in temperate deciduous forests. This issue, as well as other issues concerning the application of the CoupModel, in the present study is discussed further in Chapter 9.3.

9.3 Methodological considerations

The heat dissipation technique for the measurement of xylem sap flow in trees (Granier 1985, 1987) has been used in many species and is a method widely accepted for the quantification of transpiration (Granier et al. 1996, 2000a, Wullschleger et al. 2000, Oren and Pataki 2001, Vincke et al. 2005). The probe is small and integrates over a limited part of the sap wood thus to quantify the spatial variability in a tree stem it may

be necessary with several probes. Oren et al. (1999a) found different sap flow rates on the north and south sides of tree stems. Preliminary sap flow measurements in SOR_{MAN} (Mikkelsen, unpubl. data) showed that aspect did not influence sap flow rates. Though sap flow rate may not vary systematically with aspect in European beech, more than one sensor in each tree, as applied here, would have improved the individual tree measurements. The natural forest was characterized by a large range in trees size and exposure. Trees grown in open situations have been found to differ in their radial variation in sap flow relative to trees in a closed stand (Lang 1999, Cienciala et al. 2002). Thus, the radial measurements conducted in this study would have benefited from a higher spatial resolution i.e. trees differing in size and position in the canopy. However, the measurements were conducted on vital mature trees in the main canopy, trees assumed to contribute with a large proportion of stand transpiration. Averaging these four profiles should give a sufficient representation of this size of trees. In future studies, tree sap flow and transpiration measured in the present study could be compared to simulated tree transpiration to further investigate the relationship between transpiration, environmental variables and tree social position. Using a spatially explicit model as for example STANDFLUX may be relevant (Falge et al. 1997).

When comparing four different methods for the estimation of evapotranspiration, Wilson et al. (2001) suggested that sap flow measurements may generally underestimate transpiration, probably caused by the difficulty in scaling from measurement to the stand and catchment level in mixed species stands with a high proportion of ring-porous species. When the gradient in sap flow rate within the length of the measurement probe is large, Clearwater et al. (1999) found that the measured sap flow rate is systematically underestimated. Granier et al. (2000a) did not find that sap flow measured canopy transpiration was low compared to total evapotranspiration measured by eddy-covariance, thus, in European beech there is no need to suspect a systematic underestimation. However, seen from the diverging results on common ash (i.e. Hölscher et al. 2005, Stöehr and Lösch 2004) as well as the results of Wilson et al. (2001) and Clearwater et al. (1999) a different method or a more careful application of the heat dissipation method should have been applied for this species.

The heat dissipation method relies on measured temperature differences both at night for the determination of zero flow and during the day. Temperature differences may be influenced by natural temperature gradients in the stem and in the xylem water (Köstner et al. 1998, Do and Rocheteau 2002). Correction of sap flow measurements for the influence of natural gradients (Lundblad et al. 2001) may be relevant in future studies. Sap flow may lag behind canopy transpiration. Schäfer et al. (2000) found a lag of up to two hours, whereas Granier et al. (2000a) found no lag. In this study a possible lag in

sap flow measurements was investigated by correlating sap flow with measurements of *vpd* displaced in time (Granier et al. 2000a) and no lag was found at either site. There may still have been a lag not captured by this method as *vpd* measurements were not all at the canopy level and therefore not ideal. Braun and Schmid (1999) found that diurnal measurements of sap flow were dampened and therefore that daily integrated sap flow were characterized by a smaller error than diurnal values. Other problems related to the use of sap flow measurements are those of the radial distribution of sap flow in the stem which tend to change with the evaporative demand (Granier et al. 2000a). In spite of the relatively low number of probes and the difficulties inherent in the heat dissipation method, it seems that the measurements conducted for this study show results that agree with those found in other studies and a high and expected dependency on climatic variables.

Meteorological measurements could be obtained at the level of the forest canopy in SOR_{MAN}. In the two other stands measurements were at 2 m height beneath the canopy as well as outside the stand in an open space. This introduced the question as to what measurement of *vpd* to be used in the analyses of tree and stand transpiration in SUS_{NAT}. During the analyses it was observed that transpiration, sap flow and canopy conductance were closely correlated to below-canopy *vpd* as well as open-site *vpd* with only very small differences between the two. This was not unexpected as the natural forest used in this study is a narrow stretch of forest bordering open fields to the north and a lake to the south. Chen et al. (1995) found that during the day relative humidity increased and air temperature and wind speed decreased from the forest edge into the forest interior. The influence depended upon edge orientation and wind speed and was observed for up to 240 m into the closed forest. The measurement site in SUS_{NAT} was approximately 80 m from the northern edge and 200 m from the lake. Thus, wind would have blown from these edges and, in additions to gusts originating from above the canopy, probably have worked against the build-up of vertical environmental gradients in the stand (e.g. Denmead and Bradley 1985, Parker 1995). Further, both measurements of *vpd* are displaced from the canopy surface and none were ideal. Slightly closer correlations between sap flow, transpiration and canopy conductance were usually seen when using the below-canopy measurement, which is the reason why this was selected. However, the surface of the tree crowns still determines the location of the energy exchange and is usually where the largest variability in air temperature is found (Parker 1995, Holst et al. 2004). In future studies of transpiration it should be stressed that meteorological measurements should represent the canopy though this may introduce significant problems and costs in tall stands.

In the water budget simulations some of the meteorological data (T_a, RH, u) for canopy gap situations were from beneath the forest canopy adjacent to the gap. The variation during the day will differ between gap and below-canopy climates because of differences in incoming radiation and night time radiative cooling. The study of Gray et al. (2002) found that daily mean T_a did not differ between gap and control plots in the closed forest. As the gaps in the present study were small and the influence on the gap climate from the surrounding forest is expected to be large it was assumed that daily mean RH and u in the gap was well represented by observations beneath the forest canopy.

In SUS_{NAT} stand structure and soil both exhibited a large heterogeneity. Trees differed in species, size and age, vitality, canopy position and competition situation. To cover all these gradients as well as the variability in J_s within tree stems, a higher number of sap flow probes should have been applied than what was possible in this study. Here the number of probes was limited primarily by the capacity of data logger equipment and by the fact that sap flow measurements were part of a study where other processes in the water cycle were also quantified. Both acquisition and calculation of sap flow data is laborious. However, if transpiration dynamics of natural forests are to be studies in detail a higher number of probes than in the present study is needed. This will make it possible to include very old and large trees, trees of low vitality and tree species present in low numbers. Soil heterogeneity in the natural forest was evident for example from the data on soil water retention. At both sites, more soil pits would, to some extend, have solved the problem of soil heterogeneity in relation to the parameterization of the CoupModel for the simulation of water budgets. However, the protected status of the forest in SUS_{NAT} as well as the concern for other projects at both experimental sites made this irrelevant. Using tensiometers to measure soil water retention in-situ could also have improved the model parameterization.

The water balance of canopy gaps is not often simulated. Zirlewagen and von Wilpert (2001) present one example with a daily time resolution. Simulation in a monthly time resolution was made by Ritter et al. (2005b), Ritter and Vesterdal (2006) and Vilhar et al. (2005). Possibly the application of the CoupModel in this study is challenging the general purpose of the model as the microclimate in a small canopy gap is characterized by a lower incoming radiation than that usually found above a crop. The model may therefore be operating in a climatic range where it has not been validated. Here, the CoupModel, which is one-dimensional, was used in a canopy gap where the three-dimensional structure governs the microclimate and the water uptake. While the calibrations for the closed forest, edge and gap positions are all considered successful in the present study the calibration and the parameters applied are best defined for the

closed forest. Simulations in edge and gap positions have been useful to identify the importance of the horizontal processes in the water cycle near a gap i.e. the water used by edge trees and the relatively low evaporative demand in the gap itself. However, for further applications in gap situations, a number of adjustments and improvements could be relevant. It would be relevant to examine the sensitivity of the simulation results to changes in the parameters governing both microclimate and plant function, especially in gap conditions. Meteorological input may be derived using three-dimensional models (as for example STANDFLUX, Falge et al. 1997). Including two dimensions within the CoupModel could introduce interactions among canopy gap, edge and closed-forest situations where soil water is passed from one situation to the other. It could be relevant to investigate the effect of within-day and spatial variability in gap climate on evaporation relative to the use of daily mean values and spatial averaging.

In the CoupModel simulations no account was made for the spatial distribution of point source water input from stemflow or drippoints that may influence the spatial distribution of soil water (e.g. Durocher 1990, Jost et al. 2004). Ladekarl et al. (2001) found that, while stemflow was a significant point source, the spatial variability in soil water due to stemflow was counteracted by other processes (e.g. root uptake) and no special account of stemflow input was made in the calculation of stand water balance. Pilegaard et al. (2003) found that throughfall did not depend on the distance to stems of mature European beech.

The application of the CoupModel in this study resulted in relatively low simulated transpiration and high evaporation from the forest floor. The simulated annual transpiration in 2000 of 241 mm in the mature stand of European beech (RAV_{MAN}) is higher than measured transpiration in a similar stand nearby in 2001 (paper IV: 203 mm May 5-September 30, 2000). Based on simulated annual transpiration in SUS_{NAT} the differences in weather between the two years did not result in large differences in transpiration. A general underestimation of transpiration by the model is not indicated. The *LAI* of the stands used in the present study are lower than in other closed deciduous forests where soil evaporation was measured to 8-12% of stand evapotranspiration (Wilson et al. 2000, Davi et al. 2005), thus higher forest floor evaporation is warranted. A large variability in forest floor evapotranspiration has been observed. Transpiration from vegetation beneath common ash and *P. sylvestris* L. for the growing season was 20-30% of total stand transpiration (Roberts et al. 1980, Roberts and Rosier 1994). In declining pedunculate oak transpiration from herbaceous vegetation was as high as from the oak canopy or more, up to 2.9 mm daily (Vincke et al. 2005).Vertessy et al. (2001) found increasing forest floor evapotranspiration with increasing stand age. Wedler et al. (1996) found 44% of stand evapotranspition to originate from below a Norway spruce

canopy and Kelliher et al. (1992) found 10-20% of total stand evapotranspiration to originate from the un-vegetated forest floor below a temperate deciduous forest (LAI = 7 m^2 m^{-2}) in late summer. In the growing season 8.3% and annually 15.7% of total stand evapotranspiration originated from the un-vegetated forest floor in a temperate deciduous forest (LAI = 6 m^2 m^{-2}) (Wilson et al. 2000). Evapotranspiration from beneath a forest canopy is limited by the density of forest floor vegetation (e.g. Black and Kelliher 1989) and by the moisture holding capacity of the litter (Wilson et al. 2000). Incoming radiation may be important for a dry forest floor (Baldocchi et al. 2000) but Wilson et al. (2000) found litter moisture holding capacity to be a major controlling variable for evaporation. Frequent gusts may keep the forest floor well coupled to the air above the forest imposing a *vpd* higher than the equilibrium value (Kelliher et al. 1992). A moisture holding capacity of 0.5-2.0 mm has been reported for forest floor litter (Crockford and Richardson 2000, Wilson et al. 2000). The presence of woody debris and the state of decay (Gray et al. 2002) may influence the water holding capacity of the forest floor. The abundance and functionality of woody debris relative to the water cycle could be a relevant study in future investigations. An observed dense cover of spring ephemerals may also influence evaporation in spring. Frequent rain episodes warrants high interception losses as well as high evaporation from the forest floor (Crockford and Richardson 2000, Wilson et al. 2000). For the simulation period in paper V, daily P>0 mm occurred half of the days throughout the period and daily P>2 mm occurred on 28% of all days evenly distributed between growing and dormant seasons.

While there may be good reasons for the high forest floor evaporation, the specific parameterization of the CoupModel may also have influenced the result. Parameters in the model included the representation of an organic layer in the top 3 cm of the soil profile. This is often not included in other studies (e.g. Ladekarl et al. 2005, Christiansen et al. 2006). This representation may not be sufficient as the heterogeneity and possible hydrofobicity of the organic layer is not included. Further, the parameter values used in calculation of the forest floor evaporation may need changes and for this purpose calibration data will be needed.

10 Conclusions and perspectives

The aim of this study was to relate some structural characteristics to their function on the spatial scale of a canopy gap and individual tree as well as on the scale of the canopy and the stand. Conclusions from the present study are described below. This is followed by the perspectives of this study and some comments concerning the lessons learned.

10.1 Conclusions

These conclusions are based on the case-studies performed in three mature European beech dominated forests. They rest upon observations during two years without meteorological extremes in well drained and nutrient rich soil conditions in forests with a specific stand structure. The conclusions should be used according to these limitations. While stands are contrasted relative to species distribution and canopy stratification, the study does not allow for conclusions concerning these differences in forest structure in general.

From the study of the gap water cycle it is concluded that gap formation clearly increases soil water storage, throughfall and drainage, primarily in the growing season. Trees at the edge of a gap seem to benefit from the availability of soil water with the result that, during a seasonal soil drought, they can maintain relatively high sap flow rates throughout the summer in contrast to trees in the closed forest. The one-dimensional process-based water balance model CoupModel was applied in the complex setting of a small canopy gap (gap diameter/stand height: $D/H \leq 1$) to simulate the water budget in a daily time resolution. Differences between simulated drainage for closed forest and gap conditions were large possibly as a result of the high time resolution and the specific representation of gap microclimate characterized by low incoming radiation. Simulations indicated that the water use of trees at the gap edge may cause most of the variability in gap soil water storage observed during the growing season. This observation was supported by a simple spatial non-linear model predicting that water use of mature trees extends approximately 6-8 m from the tree stem and from a graphical representation over time of the measured gap soil water storage in the growing season. Further, the CoupModel simulations indicated that the water use of the vegetation in the gaps was very low regardless of the vegetation leaf area presumably because of low incident radiation. Modification of the gap effect in the direction toward restoring the hydrology of the closed forest was observed during the two years.

From the study of stand processes in the water cycle it is concluded that tree height does not influence European beech transpiration on these sites and was not a controlling factor for tree level mean stomatal conductance or for the canopy conductance in European beech. At high diurnal transpiration rates in European beech, the homogenous non-stratified canopy was subject to a slightly higher limitation in transpiration than the stratified canopy possibly due to the impact of high vapour pressure deficit. The mixed natural forest had a lower simulated annual transpiration than the monospecific managed forest possibly due to the late leaf development of common ash and pedunculate oak as well as low transpiration rates of common ash. However, lower transpiration due to other causes as for example very high age or low vitality could not be ruled out. The mixed natural forest had a higher simulated interception loss than the monospecific managed forest partly due to low stemflow of common ash.

10.2 Perspectives

The results as well as some of the difficulties experienced in this study point to some possible future studies. Stemflow of trees at gap edges and forest floor evapotranspiration including soil, litter and low vegetation was measured. The low number of measurements precludes any firm conclusions. However, high stemflow rates of edge trees relative to trees in the closed stand as well as high rates of evaporation from soil and litter relative to the forest canopy (up to 0.28 mm daily) indicates that it may be relevant to investigate these processes more thoroughly than done here. Simulations with the CoupModel point to relatively high values of evapotranspiration from below the canopy indicating that data for a detailed calibration of the model to represent this process would be beneficial for a future application. An assessment of the role of woody debris in the water storage and evaporation in forests may be a natural part of such studies.

The results in this study on the gap water cycle are based on two case-studies situated on soils developed on moraine deposits. On soils with different hydraulic properties (clay or sand) gap effects may be slightly different. The documentation of the extent of a gap effect on the water cycle in forests on clayey or sandy soils could be relevant as a reference for forest management. Future investigations of gap processes should continue until the hydrological conditions in the closed forest are re-established. If the frequency of high wind speed increases in the future climate (Alcamo et al. 2007) this may lead to more gaps forming after wind throw and the importance of processes related to water budgets in gaps will increase. In future investigations, gap water cycle should not be viewed in isolation, but should be scaled to the appropriate spatial level to identify the effects on the stand or regional scale.

A slightly lower stand transpiration from the mixed than from the pure European beech forest was found from the present study. For a forested watershed, Hornbeck et al. (1997) found an unexpected decrease in stream flow 7-12 years after clear felling or strip cutting in the Hubbard Brook experiments relative to an untreated control. This was explained by re-growth by species with a higher stomatal conductance and transpiration than species in the undisturbed forest. These decreases outweighed the initial stream flow increases entirely or in part. Thus, while the differences observed between the stands in this study were modest it may not be unrealistic that forest tree species differ in their transpiration rates and that changes in the species composition of forests may result in changes in the local hydrology. Early Danish research found that light demanding species had a higher transpiration rate than shade tolerant species (Ladefoged 1963). Low canopy transpiration may to some extend be balanced by evapotranspiration from beneath the canopy (Jarvis and McNaughton 1986, Roberts and Rosier 1994, Delzon and Loustau 2005) resulting in a relatively constant total evapotranspiration, but this is not always so (Vertessy et al. 2001). The stomatal regulation of transpiration works by maintaining constant leaf water potential or leaf relative water content under variable environmental conditions (Oren et al. 1999b) or a leaf water potential above a threshold value (Delzon et al. 2004). The stomatal sensitivity to changes in *vpd* was positively and approximately linearly related to stomatal conductance at a relatively low reference *vpd* for 40 species (Oren et al. 1999b) and 17 species (Granier et al. 2000b). That is, species with a high reference stomatal conductance showed a relatively large decrease in g_s with increasing *vpd*. Thus, differences in transpiration among species may not be constant but could vary with the weather or climate. The empirical relationship was shown to be consistent with theoretical predictions based on leaf specific hydraulic conductance in the pathway from soil to leaf and the difference in soil and leaf water potential (Oren et al. 1999b). Still it is not known why tree species differ in their regulation of transpiration (Ewers et al. 2005). While species differences were a likely explanation for differences in annual and growing season transpiration in the present study, an effect of very high tree age and possibly declining tree vitality was not entirely ruled out. More studies on the water use of different tree species and stands of different age could be an important contribution to improve the knowledge on the hydrological cycle in forests. In the case where the frequency of exceptional warm years increases (Alcamo et al. 2007) and the response of forest stands and different tree species to extreme drought becomes important (Bréda et al. 2006) such studies are even more crucial. Trees may differ in their spatial root distribution due to species (e.g. Rust and Savill 2000) and age (Dawson 1996, Zimmermann et al. 2000) and their root distribution may differ for monospecific and mixed stands (Leuschner et al. 2001). Some species may be efficient in the nocturnal

redistribution of soil water from deep to shallow soil (Warren et al. 2007). Ewers et al. (2005) stress the importance of the below ground structure for the future studies of forest transpiration.

The present study has by no means supplied the answers to close the gap of knowledge regarding the hydrological cycle of heterogeneous mature European beech dominated forests. Primarily it has shed some light on the effect of the formation of small gaps in forests on well drained and relatively nutrient rich soil and only little on the reversal of these gaps to the hydrological conditions found in the closed forest. The results on tree transpiration in the gap edge and simulations using the process-based model in a daily time resolution for gap and edge conditions are relatively new in this context. Differences, though modest, were found in the stand water budgets indicating that effects of species, age, vitality or other structural factors may need further investigation. The data sets collected should contribute to regional or European investigations and reviews in the future.

10.3 Lessons learned

At the outset of the study a key motivation was to find indicators of the stand water use efficiency for non-stratified and stratified (mixed) mature forests. As there was no attempt, or possibility, to quantify growth or primary production this was clearly an urealistic aim. Instead the study focussed on the quantification of the water cycle. Clearly a choise between the gap water cycle and the closed forest water cycle would have focused the study as well as concentrated the measurement efforts in just one of the options promoting more in-depth investigations and conclusions. This could have included an application of relevant methods to quantify plant water status and root distribution. Some measurements went well and some did not. The importance of carefull instrumentation and the value of previous experience with the chosen methods is one important lesson learned. Another important lesson is that the aim for a characterization of the total water cycle is very fragile. In the present case it was seriously impaired by the unsuccessful or apparently uncertain sap flow measurements (primarily those in common ash) and by the low amount of sap flow sensors in the natural forest relative to its heterogeneous structure. Had the study been directed toward specific processes in the water cycle relevant in the context of old and mixed forests the overall aim would have been less fragile.

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13 Appendix

Appendix 1: Photos from the experimental sites

***Suserup Forest gap**: Above left: Summer 2000 (E. Ritter). Photo taken from the gap centre toward the north. Above right: Spring 2001 including the gap maker (large stem right). Photo taken from the south-western part of the gap toward the north-east. Left: Summer 2002. Photo taken from the north toward the gap centre and the gap maker.*

***Suserup Forest**: Left: Dead wood and closed forest conditions (M. Christensen). Right: Closed forest conditions near the canopy gap in spring 2001.*

Ravnsholte Forest: *From the gap toward the south into closed forest in summer 2002 and in winter 2002-2003.*

Sorø: *View of the stand near the flux tower in Sorø (T. Mikkelsen).*

Appendix 2: Soil water retention

Mean volumetric soil water content (vol.%) for soil samples in Ravnsholte Forest and Suserup Forest at a range of soil water potentials (pF = -log(cm water column); pF 2.0 = - 0.01 MPa, pF 4.2 = -1.5 MPa). The number of samples and the sample depth is given. The standard error of the mean is shown in parentheses.

Ravnsholte Forest							
Number and depth of samples	pF 1.0 cm 10	pF 1.5 cm 32	pF 2.0 cm 100	pF 2.5 cm 316	pF 3.0 cm 1000	pF 4.2 cm 15800	pF 4.2 cm 15800
4 (5 cm)	53.93 (2.40)	49.65 (2.78)	39.78 (1.37)	29.93 (0.66)	27.23 (0.87)	6.53 (0.8)	6.75 (1.00)
4 (14-15 cm)	44.95 (0.49)	40.48 (0.45)	28.48 (0.38)	22.28 (0.18)	17.63 (0.35)	3.30 (0.09)	3.50 (0.11)
4 (45-55 cm)	31.68 (1.71)	29.23 (1.56)	25.8 (1.49)	22.6 (1.11)	19.3 (0.75)	4.85 (0.58)	5.05 (0.48)
4 (75 cm)	32.15 (1.00)	29.7 (1.19)	26.93 (1.56)	24.6 (1.72)	21.35 (1.67)	6.1 (0.63)	6.15 (0.60)
4 (95-100) cm	31.43 (1.13)	28.23 (2.27)	21.60 (4.07)	14.10 (4.97)	10.00 (4.72)	2.58 (1.25)	2.55 (1.26)
Suserup Forest NE							
4 (8-10 cm)	42.15 (0.90)	37.13 (0.91)	28.03 (0.91)	20.30 (0.80)	16.90 (1.16)	4.35 (0.09)	4.60 (0.07)
4 (20-22 cm)	39.65 (2.51)	32.98 (2.46)	24.40 (1.81)	17.43 (1.35)	14.00 (1.22)	4.03 (0.17)	4.25 (0.21)
4 (36-45 cm)	33.78 (0.50)	27.75 (0.50)	22.08 (0.68)	16.30 (0.99)	13.23 (1.04)	3.70 (0.58)	3.83 (0.62)
6 (82-95 cm)	28.88 (1.86)	26.55 (1.64)	23.50 (1.52)	21.22 (1.32)	19.52 (1.23)	5.72 (0.99)	5.78 (0.99)
Suserup Forest NW							
4 (7-9 cm)	44.9 (1.01)	37.28 (1.87)	28.13 (2.34)	20.90 (1.50)	17.45 (1.48)	4.55 (0.4)	4.78 (0.38)
5 (25-28 cm)	39.78 (2.33)	32.32 (2.06)	23.58 (1.81)	17.34 (1.5)	13.96 (1.34)	3.54 (0.1)	3.64 (0.11)
4 (48-53 cm)	31.68 (1.22)	26.00 (1.50)	20.93 (1.75)	16.60 (1.82)	14.97 (1.80)	5.00 (1.31)	5.03 (1.28)
5 (96-103 cm)	39.02 (1.24)	36.16 (1.20)	13.82 (1.64)	8.66 (1.95)	7.56 (1.78)	2.26 (0.52)	2.36 (0.54)

Paper I

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Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark

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Abstract

A renewed interest in natural gap dynamics has developed from a recent focus on sustainable forestry in Europe. To improve our understanding of the role of a canopy opening on the physical environment in a natural forest, a case study was undertaken in and around a gap in a semi-natural, beech-dominated (*Fagus sylvatica* L.) forest. Spatial and temporal variations in photosynthetically active irradiance (I_P), soil and air temperature (T_S and T_A) and soil water content (SWC) were studied until the third growing season after natural formation of the gap.

I_P was highest in the northern part of the gap and in the adjacent forest, particularly around mid-summer and on sunny days, when I_P was predominantly direct. Total I_P in the southern part of the gap and along gap edges declined by about 19.6% from the first to the second year after gap formation, possibly due to growth of canopy and sub-canopy trees. Maximum and mean T_S were generally highest in the southern central part of the gap, and in late spring and summer also under the closed canopy east of the gap. The insulating effect of dense regeneration could to some extent explain the spatial variation of T_S, though this was not tested directly. SWC in the gap was near field capacity and generally higher than that under the closed canopy during summer. A decrease in SWC from the first to the second year after gap formation may have been attributed to released edge trees, although water use by the dense regeneration could not be ruled out.

In general, the effect of this small irregular gap on light, soil and air temperature, and soil moisture was influenced by the considerable microsite variation. Furthermore, growth of regeneration and edge trees, resulting in increased interception, shading and water extraction by roots, may have modified the gap effect seen as early as the second year after gap formation.

Keywords: *Fagus sylvatica* L.; Forest gaps; Microclimate; Photosynthetically active irradiance; Soil moisture; Temperature

1. Introduction

The overall structure and vegetation dynamics of natural beech-dominated (*Fagus sylvatica* L.) forest

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ecosystems in Western Europe have been described in several studies in recent decades (Koop and Hilgen, 1987; Emborg et al., 1996; Pontailler et al., 1997; Wolf, 2002). These studies are an important documentation of patterns of succession in natural forest ecosystems, and they have made vital contributions to the renewed interest in nature-based forest management and conservation (Bradshaw et al., 1994; Larsen, 1995; Kilian and Fanta, 1998; Führer, 2000). A common feature of these alternative management approaches is the emphasis on natural dynamics and processes in order to obtain stable and self-sustaining forest systems (Attiwill, 1994; Hockenjos, 1999). They often aim to develop a structural variation similar to that found in natural temperate forests, mainly created by small-scale disturbances like canopy tree mortality or windthrow of small groups of trees (Emborg et al., 2000).

While many of these studies concentrate on forest structure and vegetation dynamics alone, microclimatic conditions and water fluxes also play an important role in ecological processes. Microclimate determines, among other factors, if and how well natural regeneration is established after a disturbance that gives space for a new generation of trees (Watt, 1947; Wales, 1972; Madsen, 1994, 1995; Dai, 1996; Madsen and Larsen, 1997; Heinemann et al., 2000). It affects nutrient release through decomposition and mineralization processes (Prescott, 2002) and, together with water fluxes, the loss of nutrients from the forest system (Vitousek et al., 1979; Bartsch et al., 1999). All these parameters, their temporal and spatial variation, and their complex correlation have to be considered in alternative management approaches.

Temporal and small-scale spatial variation in microclimate and soil moisture in and around canopy gaps has often been studied in managed forests (e.g. Bauhus and Bartsch, 1995; Bartsch, 2000) or in natural forests with a different climate and species composition to that found in beech-dominated forests of Europe (Canham, 1988; Gray and Spies, 1997; Wright et al., 1998; Gray et al., 2002). Similar studies in natural beech forests of Western Europe are rare, although older investigations give a valuable reference (Slavík et al., 1957, in Geiger et al., 1995). A more detailed description of our old-growth or natural temperate forest ecosystems is necessary to establish a link between knowledge of the overall forest dynamics to the process level where regeneration and nutrient- and water cycles are understood (Hüttl et al., 2000). This includes a better insight into the relationship between different microclimatic parameters in and around canopy gaps. The manifold and often contrary results reported from gap studies indicate that it is difficult to make generalizations. Case studies are necessary to give a more detailed picture of the range and variation found in microclimate and soil moisture.

The aim of this study was to describe temporal and small-scale spatial variation in microclimate and soil moisture levels in and around a small canopy gap in a semi-natural beech-dominated forest in Denmark. The focus was on gradients along the forest-gap continuum and to suggest causes of these gradients in the first 2–3 years following gap formation. We hypothesized that the creation of a canopy gap would result in increased light levels, and subsequently soil and air temperatures, particularly in the northern part of the gap. In addition, we expected soil moisture levels to be higher throughout the entire gap area than those in the surrounding forest. This work was part of a larger investigation of gaps in beech-dominated forests in Denmark and forms the foundation for studies of regeneration, nitrogen availability, nematode populations, water dynamics and diversity of fungi. It should be noted that we know of no other studies which have investigated the effect of gap formation on microclimate and soil water conditions in the same temporal and spatial detail as the present study.

2. Materials and methods

2.1. Study site and experimental design

Investigations were carried out from June 2000 to October 2001 (light and soil moisture) or May 2002 (temperature) in a gap created naturally in Suserup Forest in December 1999. Suserup Forest, located on central Zealand (55°22′N, 11°34′E, 19.2 ha), is one of the few semi-natural forests left in Denmark. It is a mixed deciduous forest with a stand basal area of 40 m^2 ha^{-1}. European beech (*F. sylvatica* L.) and common ash (*Fraxinus excelsior* L.) dominate (56.1 and 28.1% of basal area, respectively), but also several pedunculate oak (*Quercus robur* L.) and Wych elm (*Ulmus glabra* Huds.) are present. Leaf area index of

the closed canopy is approximately 5.5 $m^2 m^{-2}$ (unpublished data). The soil is nutrient rich and developed on glacial deposits, and smaller patches of sandy till occur within the dominating loamy till material (Vejre and Emborg, 1996). Stone content is very variable and ranges from about 5 to 10%. For a more in-depth description of Suserup Forest, see Emborg (1998), Emborg et al. (1996, 2000) and Fritzbøger and Emborg (1996).

The climate is cool-temperate with a mean annual temperature of 8.1 °C and a mean annual precipitation of about 650 mm, the majority of which falls in late summer and fall. The summer of 2000 was slightly cooler (15.4 and 15.7 °C in July and August, respectively) and the summer of 2001 was slightly warmer (17.9 and 17.2 °C for July and August, respectively) than the 30-year mean. The summer of 2000 and July 2001 were slightly drier than the mean, while August 2001 was wet and characterized by several very heavy rainfalls. During winter 2000–2001 and spring 2001, the lowest mean minimum temperature was −2.7 °C measured in February 2001. The lowest mean minimum temperature in winter 2001–2002 and spring 2002 was −2.8 °C, measured in December 2001, while in all other months of this period, monthly minimum temperatures remained above freezing.

The gap was irregularly shaped with a diameter of about 24 m (Fig. 1). The crown opening was estimated at approximately 18 m. Average canopy height (based on tallest 10% of the trees in the study area) was estimated at 31 m (unpublished data). The gap was formed in a severe storm on 3 December 1999 when a beech tree (diameter at breast height: 141 cm) lost most of its crown and a number of smaller trees were windthrown. The beech tree was standing approximately 5 m west of the gap centre, and its stem and the few remaining branches continued to shade parts of

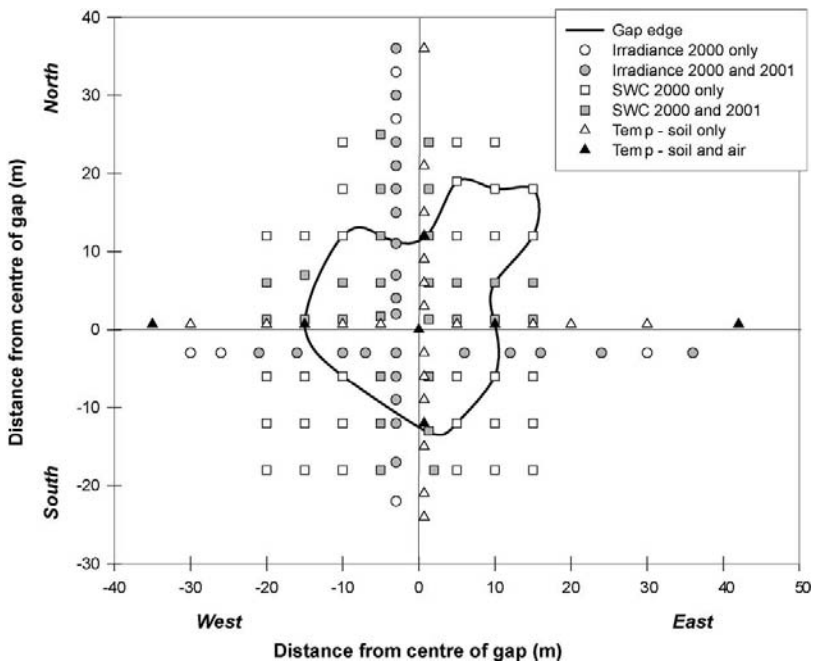

Fig. 1. Location of measurement plots at the gap site in Suserup Forest. The black line indicates the approximate contour of the gap. Photosynthetically active irradiance (circles) and soil- and air temperatures (triangles) were measured along two transects, while soil water content (squares) was measured in a grid. Note that the number of measurement plots for irradiance and soil water content changed from 2000 to 2001.

the gap after formation. None of the windthrown trees were subsequently removed from the gap due to the protected status of the forest. All of the above factors contributed to a high degree of microsite variability throughout the gap. The gap and some adjacent forest were fenced in March 2000 to avoid browsing by deer at the study site. Since microclimatic and soil moisture conditions prior to gap formation were unknown, gap effects were based on the assumption that pre-gap conditions were represented by measurement plots below the closed canopy.

Measurements discussed in this paper include photosynthetically active irradiance, soil and air temperature, and volumetric soil water content (SWC). Irradiance and temperature were measured along two perpendicular transects, while soil water content was measured in a grid design (Fig. 1).

2.2. Photosynthetically active irradiance

Photosynthetically active irradiance (I_P) was measured in 30 plots along the two transects from 13 June to 7 November 2000 and in 24 plots from 11 May to 30 October 2001 (data from 14 September to 3 October missing). I_P was determined as the photosynthetic photon flux fluence rate ($\mu mol\ m^{-2}\ s^{-1}$) in the 400–700 nm waveband and was measured by spherical sensors constructed using gallium arsenide phosphide photodiodes (G1126-02, Schottky, Hamamatsu Photonics, Japan) placed inside table tennis balls (Aaslyng et al., 1999; Einhorn et al., 2004). Two sensors were placed approximately 50–75 cm above the soil surface (just above the regeneration) in each plot. I_P was logged every 10 s, and the 10-min average was stored in a datalogger (DL2, Delta-T Devices Ltd., Cambridge, UK). On 9 August 2000, I_P was logged every 10 s, and the 1-min average was stored to give a more detailed picture of the dynamic light environment in and around the gap on a sunny day. In addition, one sensor was placed on a weather station located on an open field approximately 300 m north of the forest stand. Data are presented either directly as the mean of 10- or 1-min averages or as the integrated daily I_P ($mol\ m^{-2}\ day^{-1}$). It should be noted that although light was measured as photosynthetically active irradiance, we use it here as an indirect measure of net radiation reaching the gap and forest understorey. The ratio of photosynthetically active to total shortwave radiation (300–3000 nm) was found to vary between 0.42 and 0.59 through the course of the day above a Sitka spruce stand, while total shortwave radiation was linearly correlated to net radiation (Landsberg et al., 1973). An average of 45% of total incoming solar radiation is in the photosynthetically active range, depending on the angle of the sun and the degree of cloud cover (see Larcher, 1995).

2.3. Soil and air temperature

Teflon temperature sensors (PT-100, 210 mm × 60 mm, Delta-T Devices Ltd., Cambridge, UK) were placed at a depth of 5 cm in the mineral soil in 20 plots along the two transects to measure soil temperature (T_S). In 7 of the 20 plots – at the gap centre, under the closed canopy (35 m west and 42 m east), and at the four edges – air temperature (T_A) was measured 15 cm above the soil surface. Air temperature sensors were surrounded by radiation screens (Aanderaa, Nestun, Norway) to protect the temperature probe from solar radiation. Temperatures were measured every 3 min, and the 3-h averages were logged automatically by a stationary computer (QUATECH, Hudson, OH, USA). Only the mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) of 3-h temperature averages for each completely reported day (24 h) were used in data analyses. All temperature data presented here were obtained from October 2000 to May 2002. Due to technical problems, all soil temperature measurements after 7 May 2002 have been excluded from the analysis. The time series was also interrupted for longer periods from 15 March to 24 April 2001 and 1 January to 28 February 2002.

2.4. Soil moisture and precipitation

Volumetric soil water content in percent along 14, 30, 50 and 90 cm depth profiles was obtained using time domain reflectometry (TDR) (Topp et al., 1980; Ledieu et al., 1986). Probes consisted of two parallel steel rods of the respective lengths (diameter, 6 mm; distance, 5 cm) inserted vertically into the soil from the undisturbed soil surface. The 14 cm depth profile was measured by 20 cm probes inserted at a 45° angle. The maximum distance between probes of different lengths in the same plot was 1 m, though for most of the plots, the distance was less than 50 cm. SWC was

measured twice a week from 16 June to 31 October 2000, one to four times a month from November 2000 to April 2001, and again twice a week from 3 May to 31 October 2001. Measurements were carried out using a portable TDR cable tester (Tektronix 1502C/1502B, Tektronix Inc., Berkshire, UK). Data were collected onto a hand-held computer (Husky FS/2, Coventry, UK) and converted to volumetric water content using the calibration of Topp et al. (1980) embedded in the software AUTOTDR (Thomsen, 1994). No correction for stone content was made. For each plot, field capacity was estimated from the mean of measurements for January through April 2001. Data are presented as observed values or periodic means of SWC along the entire length of the probes (e.g. SWC_{50}) or as periodic means of the estimated SWC in a specified soil layer (e.g. $SWC_{30–50}$). The latter is calculated by subtracting measurements from two probes of different length. When soil moisture and precipitation data are presented as the mean of either gap, forest or edge conditions, these are defined as follows: plots were assumed to represent gap conditions when they were located under open sky or at least 1.5 m from the closest canopy tree bordering the gap ($n = 10$). Plots more than 1.5 m from a tree bordering the gap (in the direction away from the gap) represented forest conditions ($n = 10$). These plots were assumed to be in lee of edge trees, thus not influenced by precipitation falling at the gap edge. Remaining plots represented edge conditions ($n = 8$).

Precipitation was measured 1 m east of every SWC plot using white plastic funnels (diameter, 11.8 cm) placed 1 m above the soil surface. Water was collected in bottles inserted about 30 cm into the soil below a plastic cover to keep samples cool also during the summer. The amount of precipitation was measured weekly to the nearest ml and corrected for wetting loss (Vejen et al., 2000) relative to the inner funnel surface. Reference precipitation was measured using a Pronamic raingauge (diameter, 16.0 cm) placed on a nearby field and corrected for losses due to wind and wetting (Vejen et al., 2000).

2.5. Vegetation cover

Percent cover of ground vegetation and average height of regeneration were estimated twice during the study period: in October 2000 and June 2002. The 2002 record comprised a few more plots along the north–south transect than the 2000 record, which explains the missing values for October 2000 in Fig. 9. Ground cover in October 2000 was divided into four classes (0, 0–25, 25–50 and 50–100%) of which the midpoint is displayed in the figure. For June 2002, the absolute value of the estimated plant cover in percent is illustrated in the figure.

2.6. Statistical analyses

To test for plots with similar I_P or temperature regimes, one-way ANOVA with repeated measurements followed by Tukey pairwise multiple comparisons (SigmaStat, Version 2.03, SPSS®, Chicago, Illinois) were applied to the following data: (i) mean integrated daily I_P for 2-week periods; (ii) 10-min (1-min for most of 9 August) averages of I_P for 2-h intervals on a sunny (9 August 2000) and an overcast (10 August 2000) day; (iii) daily $T_{S,max}$, $T_{S,mean}$, $T_{A,max}$ and $T_{A,mean}$ by month; (iv) daily differences between $T_{S,max}$ and $T_{S,min}$ by month. Day of the month ((i), (iii), (iv)) or time of the day (ii) were used as the repeated measurement. When equal variances or normal distribution could not be achieved by transformation, a Friedman Repeated Measures ANOVA on ranked data was conducted. All I_P data were tested as ranked data.

The effect of year (2000 versus 2001) on average daily integrated I_P for the time period 14 June–13 September (longest uninterrupted time period in common for both years) was tested using a Student's *t*-test between years by plot. I_P was not measured in six plots in 2001 (see Fig. 1), so these plots were excluded from the analysis. The effect of season on differences between daily $T_{S,max}$ and $T_{S,min}$ were analysed by the GLM procedure of the SAS statistical software, and the correlation between T_S and T_A by the CORR procedure which calculates Pearson correlation statistics (Version 8.2, SAS® Institute Inc., Cary, NC, USA). The factor *season* had three levels: (i) when trees were without leaves (November–February), (ii) when leaves were developing (March–May), and (iii) when canopy trees were in full leaf (June–October). All statistical tests were considered significant when $P < 0.05$.

3. Results

3.1. Photosynthetically active irradiance

The distribution of I_P in and around the gap was generally much more variable through the day on a sunny day than on an overcast day (Fig. 2). Between 6:00 h and 8:00 h, the distribution of I_P in and around the gap was very similar on both days, showing that light was still predominantly diffuse 50–75 cm above the soil surface. At this time of day, I_P was only slightly higher in the gap compared to areas below the forest canopy, particularly south of the gap. As the angle of the sun increased through the day, total I_P increased on both days. However, on the overcast day, the distribution of I_P remained highest in and just north and east of the gap. On the sunny day, the distribution of I_P in the gap and surrounding forest was much more dynamic, probably as a result of sunflecks and sun patches caused by this and other gaps in the canopy outside the study area. From 8:00 h to 10:00 h on 9 August (sunny day), the 2-h mean I_P was, in fact, highest in the plot 36 m north of the gap centre, which could be attributed to an opening in the canopy to the east of this plot, outside the fenced study area. By midday, when the angle of the sun was highest, I_P was highest at the northern edge of the gap and in the northern part of the gap itself. The intensity of I_P was much higher on 9 August (average 15 m north = 1430 μmol m^{-2} s^{-1}) than on the following

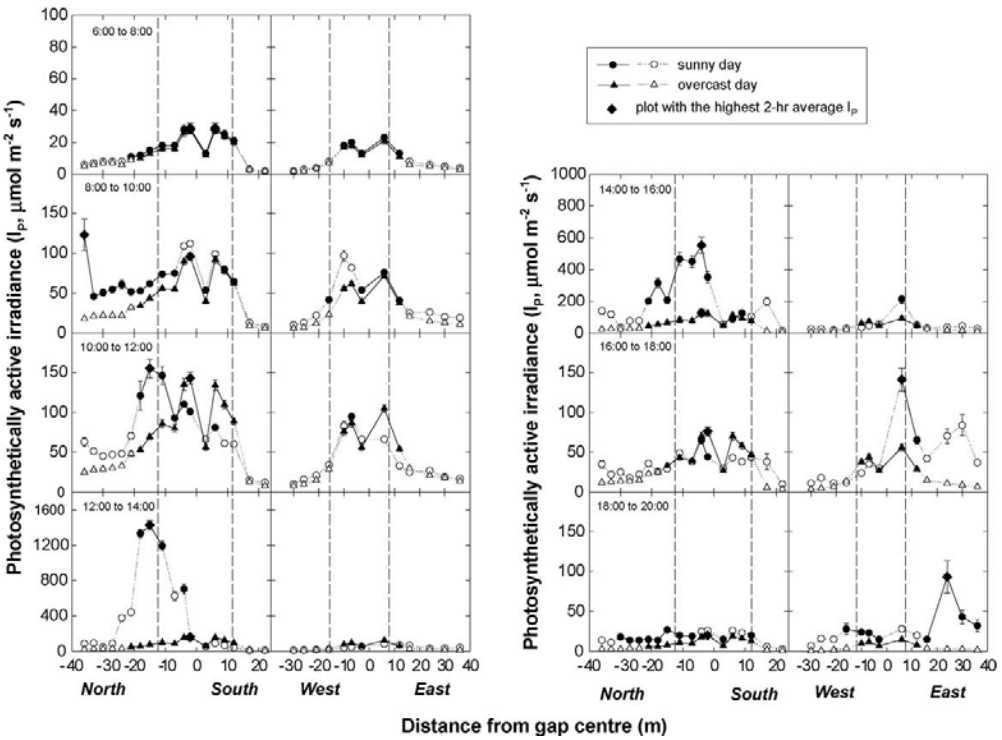

Fig. 2. Average photosynthetically active irradiance (I_P; μmol m^{-2} s^{-1}) for 2-h intervals along the north–south and west–east transects on a sunny (9 August) and an overcast (10 August) day in 2000. Time periods represented are indicated in the upper left corner of each graph pair. Solid symbols indicate plots which were not significantly different from the plot with the highest 2-h average I_P for the given time period (Friedman Ranked ANOVA, Tukey: $P > 0.05$). Dashed lines show the approximate edges of the gap. Error bars are 1 S.E. Note difference in *y*-axis scaling between time intervals.

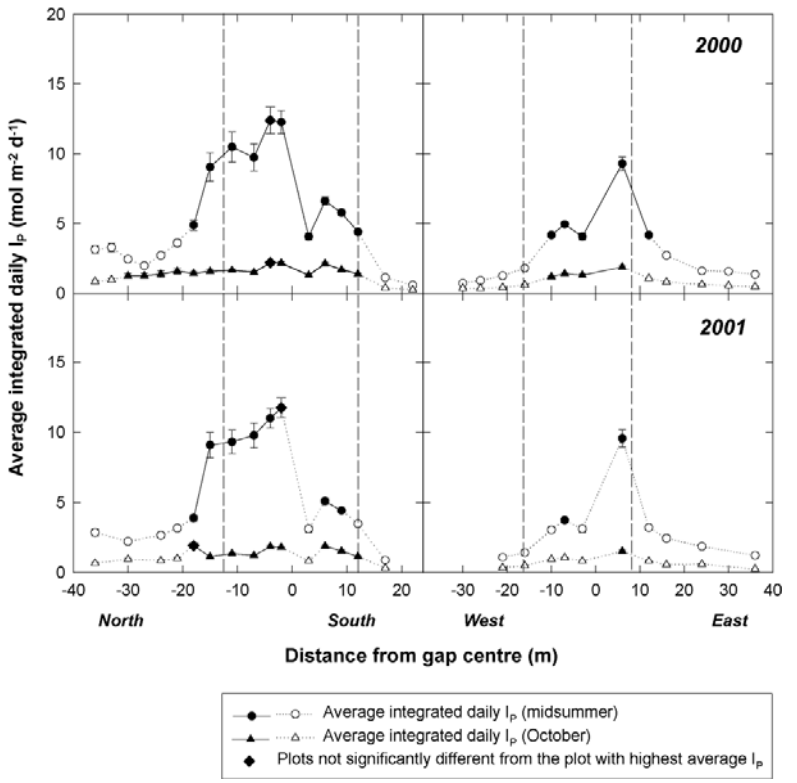

Fig. 3. Average daily integrated photosynthetically active irradiance (I_P; mol m^{-2} day^{-1}) along the north–south and west–east transects in 2000 (upper) and 2001 (lower). Time periods represented are 14–30 June 2000 (midsummer), 1–15 October 2000, 16–30 June 2001 (midsummer) and 4–29 October 2001. Solid symbols indicate plots which were not significantly different from the plot with the highest average integrated daily I_P for the given time period (Friedman Ranked ANOVA, Tukey: $P > 0.05$). Dashed lines show the approximate edges of the gap. Error bars are 1 S.E.

day when conditions were overcast (average 2 m north = 165 μmol m^{-2} s^{-1}). As the sun set to the west on 9 August, plots in the eastern part of the gap (16:00–18:00 h) and far into the forest along the eastern transect (plot east 30 m; 18:00–20:00 h) experienced the highest average I_P.

Average integrated daily I_P for 2-week periods through the growing seasons was generally higher in plots located in the gap and into the forest towards the north than in the rest of the study plots (Fig. 3). At midsummer (late June) and in early October 2000, the plot with the highest average integrated daily I_P was 4 m north of the gap centre. Plots not significantly different from this plot (Tukey: $P > 0.05$) spread further north into the surrounding forest in October than in June. At midsummer 2001, the plot 2 m north of the gap centre had the highest average integrated daily I_P, and those plots located under suppressed saplings or along the south, east or west gap edges (i.e. plots at south 3 and 12 m, west 10 m and east 12 m) received light levels significantly different from the plot at 2 m north. In both years, higher I_P in the gap and to the north decreased as autumn approached and the angle of the sun fell below the gap horizon, resulting in practically no difference in I_P between gap, edge and forest plots by October.

Fourteen of the 24 plots monitored in both 2000 and 2001 showed a significant change in average integrated

daily I_P between years for the time period 14 June–13 September (plots located at: 30, 21 and 18 m north; 3, 6, 9, 12 and 17 m south; 21, 16, 10 and 7 m west; 12 and 24 m east). These plots all experienced a decrease in light, except for the plot at 24 m east. On average, this decrease was 19.6% from 2000 to 2001, ranging from 14.3% in the plot at 18 m north to 27.8% in the plot 3 m south of the gap centre. The plot at 24 m east experienced a 39.6% increase in total I_P from the first to the second growing season due to the establishment of a sizeable gap to the south, just outside the fenced study area during the winter 2000–2001. This allowed much more light to reach this plot during the 2001 growing season than in the previous year.

3.2. Soil and air temperature

A significant effect of the gap on $T_{S,max}$ and $T_{S,mean}$ was found during all months of the measurement period. Monthly averages of $T_{S,max}$ and $T_{S,mean}$ at the centre of the gap were up to 3 °C higher than the monthly averages of all plots significantly different from the centre plot (Tukey: $P < 0.05$). The group of plots with $T_{S,max}$ and $T_{S,mean}$ equal to the centre were found within the central southern half of the gap: between the western and eastern edge and up to 5 m south of the gap centre. In most months, the area enclosing the plots with the highest $T_{S,max}$ and $T_{S,mean}$ tended to skew to the eastern part of the gap. This eastward tendency was most pronounced for $T_{S,max}$ from May to August 2001, when the area with $T_{S,max}$ similar to the gap centre continued up to 15 m into the adjacent forest (Fig. 4). For $T_{S,mean}$, this eastward expansion into the closed forest was only found from May to July 2001. No gap effect was seen for $T_{S,max}$ in November and December 2000 and in December 2001. For $T_{S,mean}$, a gap effect was seen for all months of the measurement period.

Differences between daily $T_{S,max}$ and $T_{S,min}$ in each plot throughout the study period were lowest (average, 0.8 °C) in winter when trees had lost their leaves (November–February), intermediate (average, 1.4 °C) when canopy trees were in full leaf (June–October), and highest (average, 2.4 °C) in spring when leaves were developing (March–May). This effect of season was very significant ($P < 0.0001$). Plots with high temperature differences were found in and around the centre of the gap (Fig. 5).

Throughout the measurement period, daily $T_{A,mean}$ was up to 5 °C higher and daily $T_{A,max}$ up to 10 °C higher in the centre of the gap than in the six other plots where air temperature was measured. $T_{A,mean}$ and $T_{S,mean}$ measured in the seven common plots were correlated in all months ($R \geq 0.7$), except January 2002 ($R \leq 0.2$) and May 2002 ($R \leq 0.6$). In May 2002, a correlation was found for the centre plot only ($R = 0.9$). Air temperatures were on average 1–9 °C higher than soil temperatures, though as much as 12 °C higher in early spring and 10 °C lower in winter. Winter was the period with lowest soil temperatures: from late December to the end of January (2000–2001 and 2001–2002), daily $T_{S,mean}$ remained below 5 °C. Increases in both $T_{A,mean}$ and $T_{S,mean}$ occurred earlier and decreases later in plots within the gap than those under the closed canopy.

3.3. Soil moisture and precipitation

Average field capacities ($n = 59$ plots) of the four depth profiles (0–14, 0–30, 0–50 and 0–90 cm) were 30.8, 29.7, 26.9 and 25.4%, respectively, and the highest values were found in the northwestern part of the grid. The lowest observations of SWC in both 2000 (September) and 2001 (August) were 7–8% in the 0–50 and 0–90 cm profiles in a few plots in the forest. The permanent wilting point ranged from 3.4 to 5.4% in the different soil horizons (unpublished data). During the growing season, SWC was generally highest in the gap, intermediate near the gap edge and lowest in the forest. From July to September 2000, the area in the gap with SWC_{50} near field capacity decreased with time (Fig. 6). On average, the difference in SWC between edge and forest conditions was most pronounced for the upper soil layers (Fig. 7). SWC down to approximately 50 cm depth decreased early in the season, while SWC further down in the soil profile decreased in mid- or late summer. The opposite effect was observed in fall when the upper soil layers were re-wetted before the deeper layers. These effects were most pronounced for edge and forest plots in 2001 (Fig. 7). In the northern part of the gap, SWC_{50} for July were lower in the second year than those in the first year after gap formation. This difference seems larger than the difference observed for forest conditions between the 2 years caused by differences in climate and precipitation. SWC for both years in the

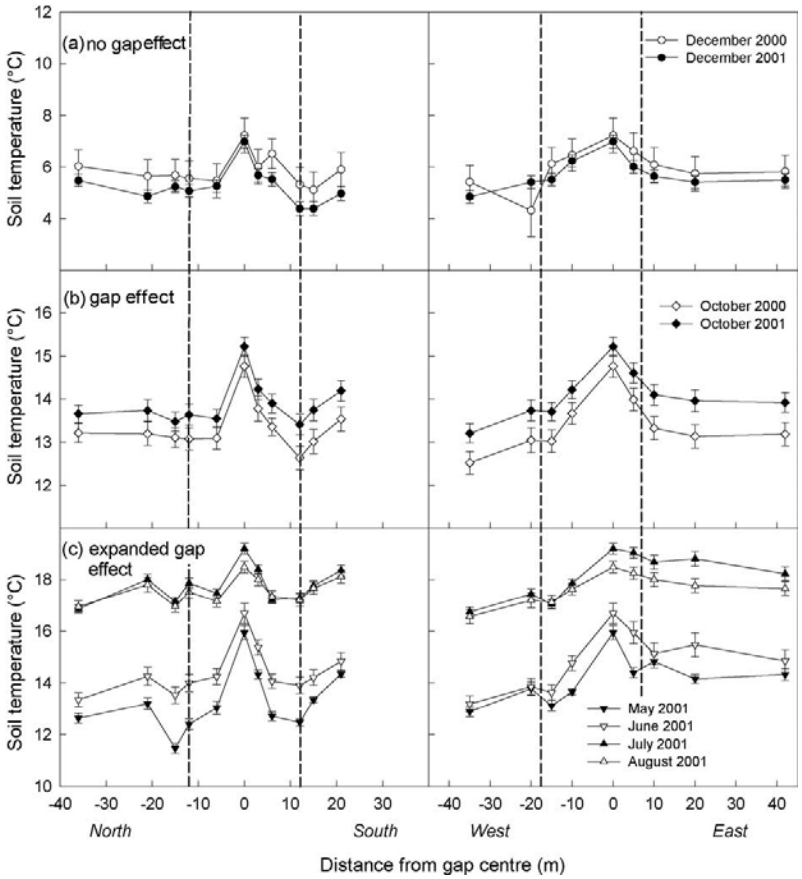

Fig. 4. Monthly averages of daily maximum soil temperatures ($T_{S,max}$) at 5 cm depth along the north–south and west–east transects in months showing (a) no clear gap effect, (b) significantly increased temperatures in the central southern part of the gap and (c) a gap effect expanded east of the gap. Dashed lines show the approximate edges of the gap. Error bars are 1 S.E.

gap centre were relatively close (Fig. 8). Transects for the driest months of the 2 years (August 2000, July 2001) show a similar pattern (data not shown). On average, gap plots were slightly drier in 2001 than those in 2000, especially below 30 cm depth (Fig. 7), which could be due to more roots present and/or a higher interception loss in 2001. In the gap, precipitation was 77% (winter) and 90% (summer), in the edge zone 79% (winter) and 76% (summer) and below the forest canopy 78% (winter) and 74% (summer) of reference measurements outside the forest. There was no consistent pattern of higher precipitation towards the eastern edge of the gap in spite of the prevailing winds from the west; spatial variability was high throughout the measurement grid. In winter, two plots at the eastern edge showed a high precipitation (above 90%). One plot was located near the remains of a tree crown from a windthrown tree which may have collected water at this plot. Near the eastern edge (in the gap), one plot showed a very low precipitation (near 50%). This plot may have been in lee of the stem of one of the windthrown trees. In summer, plots located near the gap centre showed precipitation of about 100%.

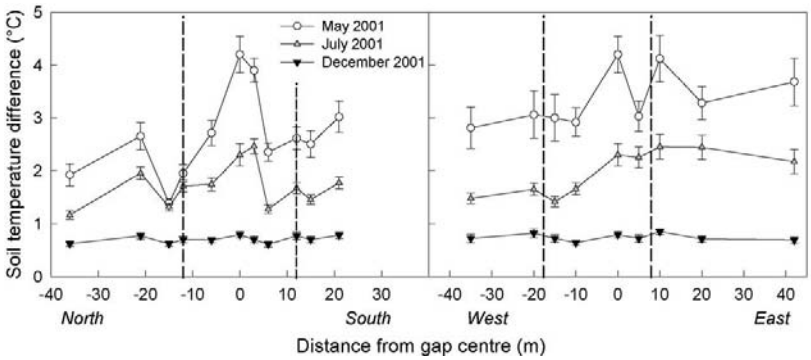

Fig. 5. Monthly average differences between daily maximum ($T_{S,max}$) and minimum ($T_{S,min}$) soil temperatures at 5 cm depth for three selected months, illustrating the periods with highest (May 2001), intermediate (July 2001) and lowest (December 2001) differences.

3.4. Vegetation cover

Regeneration potential of the study site was high, and our overall observation was that regenerating plants grew rapidly. At the end of the first growing season after gap formation (October 2000), average tree height of young regenerating trees was no more than 30 cm (Fig. 9). Vegetation cover was about 15%, except at the gap centre and in the two plots north and east of the gap centre, where it was up to 80%. In the third growing season after gap formation (end of June 2002), vegetation cover as well as plant height had increased, especially in the northern and western parts of the gap.

4. Discussion

4.1. A clear gap effect the first year after formation

The formation of a gap in Suserup Forest in December 1999 resulted in a strong increase in I_P reaching the forest understorey during the first growing season after formation. This result is in accordance with other studies in old-growth forests (e.g. Canham, 1988; Canham et al., 1990; Barik et al., 1992). I_P increased most in the northern part of the gap and below the canopy just north of the gap, which has also been reported by Wright et al. (1998) and Gray et al. (2002) for old-growth and managed coniferous forests in western North America. This effect was strongest when I_P was predominantly direct, that is, on sunny days, and when the angle of the sun was at its highest. On overcast days, when I_P was predominantly diffuse, I_P was highest in and around the gap centre. Late in the growing season (September and October), the difference in total I_P between plots in the gap and under the forest canopy was no longer significant, since the sun no longer came above the gap horizon during the course of the day. These results are supported by the general observation that the distribution of diffuse irradiance in the understorey is primarily determined by the geometry of the canopy opening and not by the position of the sun (Canham et al., 1990; Ackerly and Bazzaz, 1995; Gray et al., 2002). In contrast, measurements of direct-beam radiation in five temperate and tropical forest types showed a much greater spatial and temporal variability than diffuse radiation (Canham et al., 1990), similar to the pattern seen in Suserup Forest. On a sunny day (9 August 2000), light conditions were very variable and small openings in the canopy resulted in sunflecks creating a very different distribution of I_P than that on an overcast day (10 August 2000).

A clear effect of the gap could also be seen on SWC during the 2000 growing season. As summer progressed, soil moisture was clearly higher in the gap than that in the forest. This has also been found in pure European beech forests (Bauhus and Bartsch, 1995), a mixed deciduous forest (Slavík et al., 1957, in

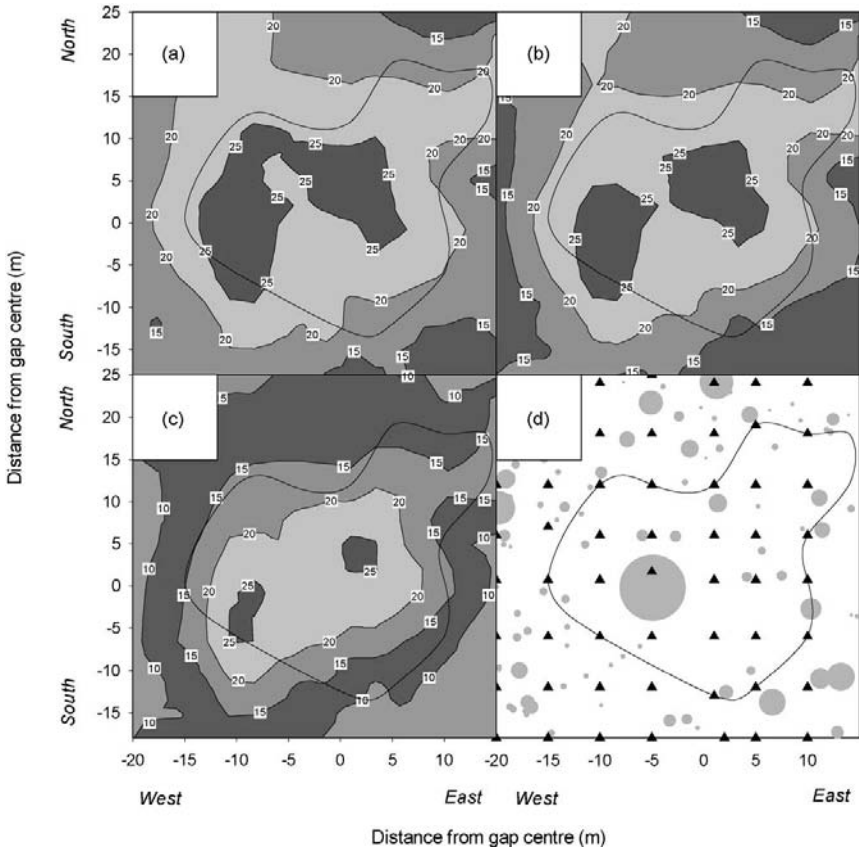

Fig. 6. Soil water content (%) at 0–50 cm depth (SWC_{50}) in and around the canopy gap in the summer of 2000. Numbers in the graphs show the border between zones of similar SWC_{50}: (a) mean for July ($n = 7$); (b) mean for August ($n = 9$); (c) lowest observation, 1 September; (d) location of larger trees in and around the gap. The diameters of circles do not correspond to tree diameters but indicate the relative size of the trees. The gap centre is at (0 m, 0 m). A thin black line indicates the edge of the gap. The contour plot is based on 59 observations and data are smoothed using a negative exponential weighting procedure with fixed bandwidth and a sampling proportion of 0.2.

Geiger et al., 1995), coastal Douglas-fir forests (*Pseudotsuga menziesii* (Mirb.) Franco) (Gray et al., 2002) and for some tropical forests (Veenendal et al., 1996; Ostertag, 1998). These studies represent both managed and old growth forests. Higher SWC in the gap than that in the surrounding forest was probably due to both an increase in precipitation and a decrease in transpiration in the gap (Zirlewangen and von Wilpert, 2001). In our study, precipitation was higher in gap than in that forest conditions (90 and 74% of reference precipitation, respectively). This difference is the equivalent of approximately 36 mm rain from mid June to September 2000. Water extraction by trees was expected to decrease in the gap as the leaf area and therefore transpiration were reduced and root gaps may have formed (Nielsen and Mackentun, 1991; Müller and Wagner, 2003). This is supported in our study by the vertical profiles of SWC during the summer for gap and forest, respectively. In the summer 2000 (mid June–September), transpiration from the closed forest accounted for approximately 144 mm (L. Dalsgaard, unpublished data) at the measurement site. This loss can be expected to have been fully or partly absent in the gap. For a European

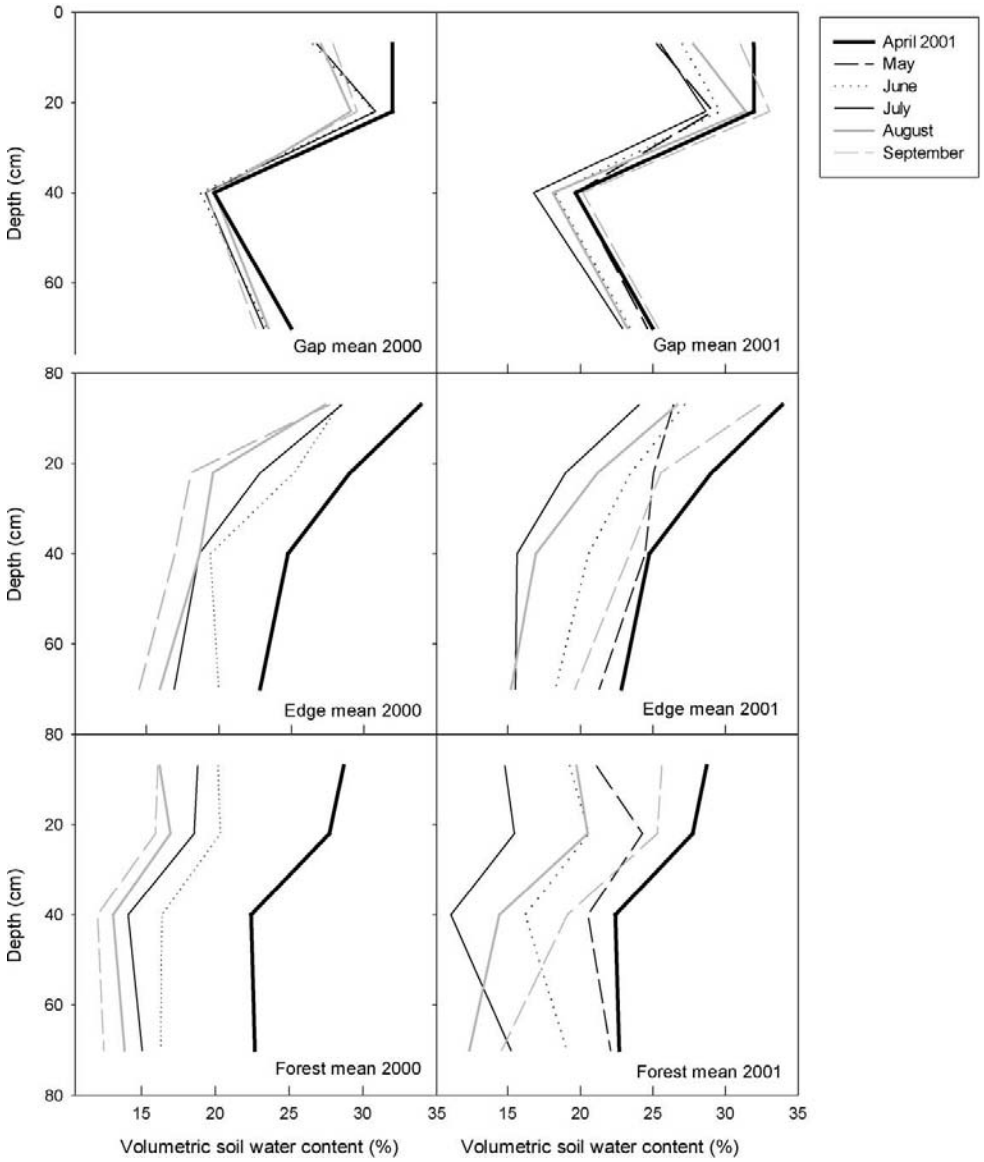

Fig. 7. Vertical profiles of the monthly mean soil water content (%) for gap ($n = 10$), edge ($n = 8$) and forest ($n = 10$) conditions in June–September 2000 and 2001. Depths represent the midpoint of the following volumes: 7 cm, $SWC_{0–14}$; 22 cm, $SWC_{14–30}$; 40 cm, $SWC_{30–50}$; 70 cm, $SWC_{50–90}$. April 2001 represents field capacity.

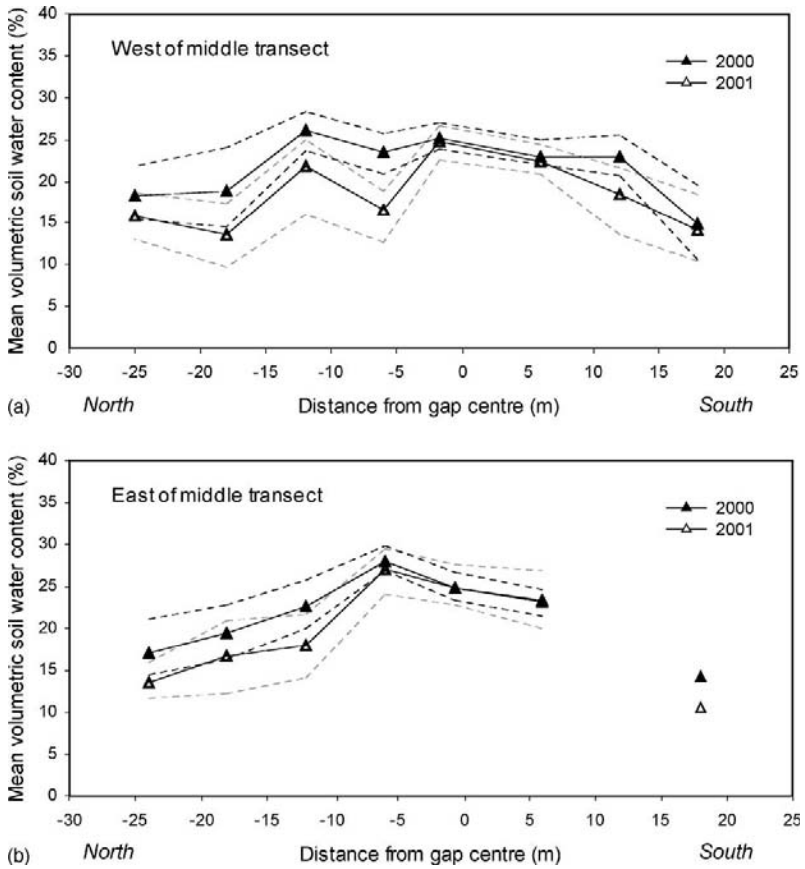

Fig. 8. Mean volumetric soil water content (%) of 50 cm deep soil profiles along transects located (a) west and (b) east of the north–south transect running through the approximate centre of the gap, measured in July 2000 (black triangles) and July 2001 (white triangles). Dotted lines indicate the maximum and minimum values.

mixed forest, it was found that the most important contribution to the differences in soil moisture between forest and gap conditions was the lower interception loss in the gap (Zirlewangen and von Wilpert, 2001). The approximate figures for transpiration and interception loss given above for our measurement site suggest that a major cause of the gap–forest difference in SWC was the lack of transpiration in the gap. The spatial transition in SWC from forest to gap was relatively abrupt, possibly due to a high competition for below-ground resources in the stand (high basal area). If this was the case, fine roots would tend not to extend as far from the stem as in stands with less intense competition (Ammer and Wagner, 2002).

Precipitation in the gap did not show higher values near the eastern edge as found in early studies (Slavík et al., 1957, in Geiger et al., 1995). The prevailing wind direction is west; thus, such a pattern could have been expected. This is probably because our gap was very irregular and drip points from trees at the undulating gap edge, fallen crowns and stems of fallen trees influenced the spatial pattern within this very small canopy opening. Also, the rough canopy could

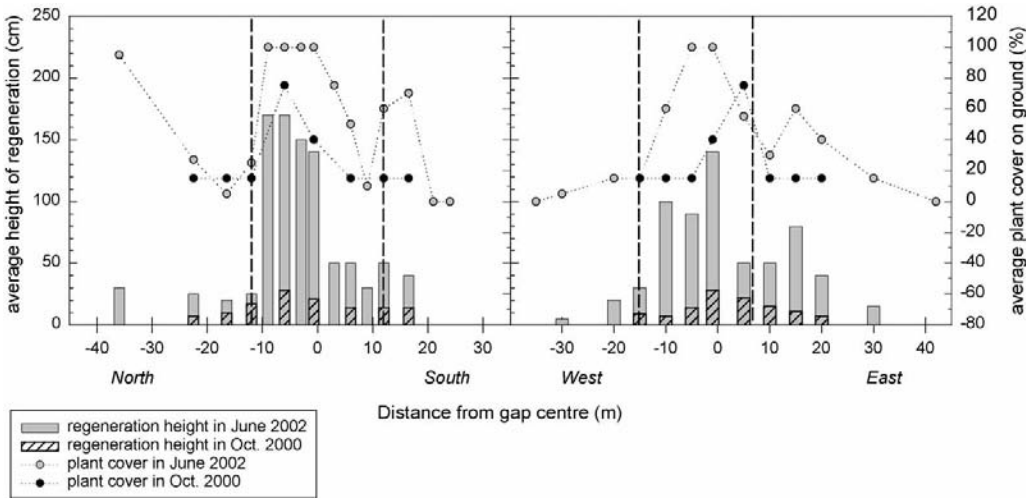

Fig. 9. Ground cover of vegetation in percent (circles) and average height of regenerating trees (predominately *Fraxinus excelsior* L.; bars) at the study site in Suserup Forest. Black circles and outlined bars refer to October 2000, grey circles and grey bars to mid-June 2002 (a few more plots than those in 2000).

have altered the overall pattern of wind direction above the gap.

Soil temperature measurements were only available for October during the first growing season. In this month, however, the effect of the gap was seen as increased soil temperatures in the central and southern part of the gap. This effect disappeared after leaf fall in November, when the canopy became more open and differences between light conditions and the insulating effect of the canopy became less distinct between gap and forest (Carlson and Groot, 1997).

4.2. Gap effects modified in the second and third years after formation

As the gap aged, effects on I_P and SWC that were apparent in the first growing season became less clear. Although not tested directly in the present study, this could in part be a result of the intense growth of regeneration, particularly in the northern part of the gap. Spatial variation in I_P caused by the advancing regeneration was essentially excluded because sensors were kept above the regenerating canopy, and therefore light measurements continued to be influenced only by the canopy opening. However, an earlier study in the same forest has shown that light levels below a regenerating ash canopy fell from an average of about 10% of full sunlight in a newly formed gap to just 3% below the regenerating canopy (Emborg, 1998). Thus, we expect that I_P at the soil surface decreased as the gap studied here aged. In contrast, measurements of both SWC and soil temperatures were probably more directly affected by the growth and structure of both mature trees and regeneration. That light, temperature and soil moisture reacted differently to the canopy opening and possible modifications by growing vegetation can be seen in Fig. 10, where averages for the second growing season (May–September 2001) for all parameters are displayed together.

The high light levels measured in the northern part and north of the gap would normally result in increased soil temperatures in that area, as reported by e.g. Bauhus (1996), Wright et al. (1998) and Gray et al. (2002) in mature deciduous and coniferous forests. However, the northern part of the gap was cooler than the gap centre. Thus, one or more mechanisms must have worked to cool the soil surface or to capture the incoming radiation before it reached the ground. It cannot be excluded that the canopy of the regenerating trees growing densely in the northern

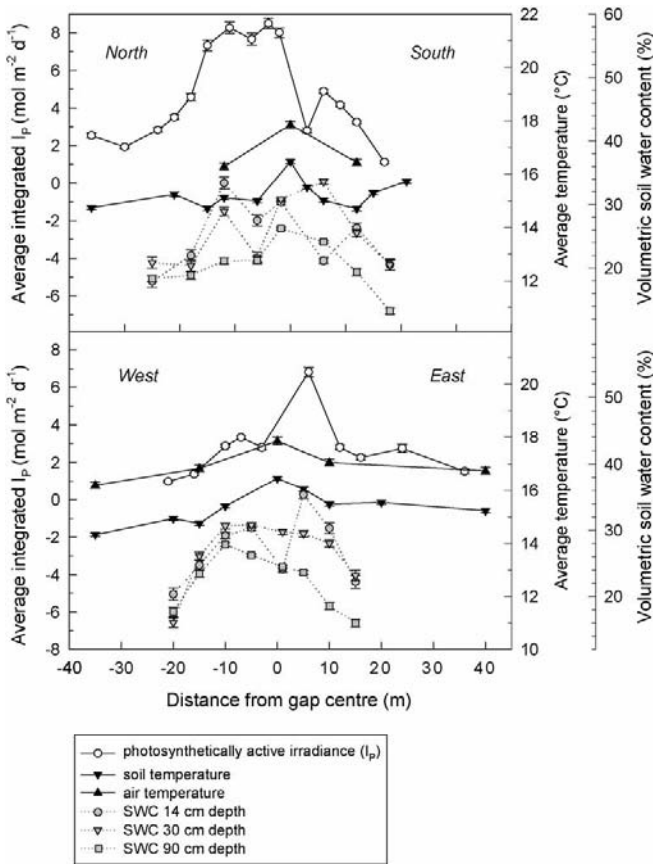

Fig. 10. Averages of photosynthetically active irradiance (I_P; white circles), soil- and air temperatures (black triangles), and soil water content along different profiles (grey symbols) along the two transects in Suserup Forest throughout the period 12 May–13 September 2001 (longest uninterrupted time period in common for all parameters). Dashed lines show the approximate edges of the gap. Error bars are 1 S.E. Note the different scales of the three parameters.

part of the gap stopped much of the incoming radiation from reaching the soil surface and cooled the air by transpiration, thereby preventing an increase in soil temperature. A shading effect of seedlings has been observed by Childs and Flint (1987). Bauhus and Bartsch (1995) attributed lower temperatures in the northern part of gaps to higher soil moisture contents. In our study, the northern part of the gap tended to have similar or slightly lower soil moisture levels than the southern part of the gap.

In the third year after gap formation, the advanced regeneration in the gap had reached a height of up to 2 m and vegetation cover was 100% in the northern part of the gap during summer 2002. Though the vegetation was not studied in 2001, it is assumed that spatial differences in vegetation density and height in 2001 are well represented by observations from 2002. A dense vegetation must be assumed to insulate during the night (Balisky and Burton, 1993; Holbo and Childs, 1987). Consequently, $T_{S,max}$ as well as the daily difference between $T_{S,max}$ and $T_{S,min}$ was lowest in the northern part of the gap.

High T_S in plots east of the gap centre in the months around mid-summer (May–August) could be attrib-

uted to the daily variation in I_P, but also an effect of the sparse regeneration and low vegetation cover in the east could not be excluded. As the angle of the sun decreased in the evening, I_P reached relatively far into the adjacent understorey as long as the sun was above the gap horizon. This effect of I_P reaching beyond the gap edge was probably more pronounced towards the east than that towards the west, since both air and soil were still cool from the previous night when the sun was at a similar low angle in the morning, shining into the understorey west of the gap (Oliver and Larsen, 1996). Furthermore, the stem and remaining branches of the large beech tree just west of the gap centre shaded the western part of the gap in the morning, while no larger stems influenced irradiance to the east. An influence of small canopy openings outside the gap area investigated cannot be excluded either.

In addition to the possible influence of regeneration, growth of canopy trees and suppressed saplings may also have modified the gap effect on microclimate and SWC with time. Total I_P in the growing season (14 June–13 September) decreased significantly from 2000 to 2001 in several plots, particularly located in the southern half of the gap (where direct sunlight only occurred as sunflecks) and along the western and eastern edges. Since no significant difference in average integrated daily I_P between the 2 years was seen in plots in the northern part of the gap itself, annual differences found in other plots could not be ascribed to differences in weather (cloud) conditions. This was supported by measurements made outside the forest (data not shown). Differences observed in edge plots could therefore be the result of lateral growth of bordering canopy tree crowns, as reported by Hibbs (1982), Valverde and Silverton (1997) and Muth and Bazzaz (2002). The 27.8% reduction in I_P seen in the plot 3 m south of the gap centre was probably due to the presence of a repressed *U. glabra* sapling that, once released from heavy shade, was able to grow and capture light more effectively. This could already be seen by late August 2000 (data not shown).

The decrease in SWC in the gap from the first to the second year after formation of the gap – in particular in the northern part during the driest weeks of the summer – was probably due to a combined effect of increased interception of precipitation and increased root extraction of water from the soil. Gray et al. (2002) ascribed low soil moisture in the northern part of a gap in a mature coniferous forest to higher evaporation from plants and the soil surface. In our gap, both regenerating trees, saplings already present as advanced regeneration before gap formation and mature edge trees may have increased their water use from 2000 to 2001, both as transpiration and rain interception. A possible increase in root extraction in the gap is supported by findings in even-aged Norway spruce (*Picea abies*) stands where rapid belowground gap closure was found for gaps less than 15 m in diameter (Müller and Wagner, 2003). The growth of roots into the gap on our site is complicated by possible species differences in rooting patterns (Rust and Savill, 2000) and competitive abilities in mixed stands (Leuschner et al., 2001; Schmid and Kazda, 2001). The interception of precipitation by edge trees is expected to increase with time after gap formation because of lateral growth of crowns towards the canopy opening (Muth and Bazzaz, 2002). However, crown expansion as well as the water transporting capacities of twigs (Lemoine et al., 2002) may be delayed for at least one season as it is necessary for the tree to acclimate to the new environmental conditions. For beech in particular, which exhibits a rather fixed growth pattern, much of the growth response observed in 1 year has been determined in the previous year (Kozlowski and Pallardy, 1997). Thus, leaf area and water use of edge trees may increase more in the second year than in the first year after gap formation, which could affect the speed of gap closure and indirectly the response of both light, temperature and SWC. SWC decreased from the first to the second year after gap formation during the driest summer month in six plots, of which four were close to large trees near the gap edge (data not shown). Therefore, it is plausible that these large trees contributed to the change in SWC with time as large trees use more water than regenerating plants can be expected to. However, differences in SWC between the two summers are difficult to interpret due to differences in the cumulative water balance (June and July were wet and cool in 2000 compared to 2001). Investigations of the whole water balance for individual plots using climate driven models could give more insight into the reasons for the observed annual differences than purely spatial patterns in SWC do.

The effect of the gap on I_P and SWC in particular observed in the first year after gap formation was less

clear already by the second growing season. Earlier studies have shown that it takes about 4–10 years for the canopy to close, depending on the size of the opening and potential for regeneration (Gysel, 1951; Valverde and Silverton, 1997), and more than 6 years for roots to exploit the root free area in small gaps (<15 m diameter) (Müller and Wagner, 2003). This is less time than needed for regenerating plants to reach the canopy. Gysel (1951) supposed furthermore that both large and small canopy openings were completely closed after 20 years. Our results suggest that the effects of a gap on microclimate may disappear much faster than this. However, long-term observations are needed to test this hypothesis and more parameters should be included to explain both spatial and temporal variability. Specifically, we recommend to include the structure and growth of vegetation at all vertical levels more closely in future studies of gap effects on microclimate and soil water.

5. Conclusion

In this structurally heterogeneous forest, characterized by a high potential for regeneration, the effect of a small irregular gap on light, soil and air temperature, and soil moisture was apparently modified by a considerable microsite variation. Furthermore, growth of regeneration and edge trees, resulting in increased interception and water extraction by roots, may have modified the gap effect as early as the second year after gap formation.

As expected, an increase in I_P in the central and northern parts of the gap and north of the gap as well as a higher SWC in the gap than that in the forest during the first growing season was observed. However, SWC approached forest conditions at many positions already in the second year after gap formation. Variability in soil temperatures could not be explained by the influence of I_P and was contrary to our expectations. We suggest that variations in soil temperature were closely connected to the shading, evaporative cooling and insulating effects of low vegetation; however, this hypothesis remains to be tested in depth. Generally, our study indicates that differences between gap and forest conditions may already decease within a few years after gap formation. Thus, if information on the large scale structure of natural forests is to be useful for the prediction of the spatial variability of microclimatic conditions, it is also necessary to consider short-term changes, including growth patterns of vegetation and the ability of plants to benefit from and to acclimate to new climatic conditions.

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Paper II

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Above and below ground gaps – the effects of a small canopy opening on throughfall, soil moisture and tree transpiration in Suserup Skov, Denmark

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In the natural temperate deciduous forest the gap-phase is crucial for forest regeneration and succession. During a relatively short time span the forest microclimate is changed with higher global radiation, larger temperature fluctuations, and less demand for soil water and nutrients from trees. These changes depend on the size and structure of the gap. This study takes a closer look at the changes in the hydrological cycle in a small canopy gap (diameter < stand height) in Suserup Skov during the first and second growing season following the gap-establishment. Specifically the effects of gap formation on throughfall, soil moisture, forest floor evapotranspiration and individual tree transpiration for European beech *Fagus sylvatica* is described. Stemflow for European beech and common ash *Fraxinus excelsior* for exposed trees and for trees in the intact forest is shown. Further, a non-linear model is used to test the significance of tree size and position on the spatial variability of water use at the soil moisture measurement positions. Throughfall was significantly higher in the gap than in intact forest positions annually (17%) as well as in summer (19–30%) and spring (19%). Soil moisture in the gap was significantly higher than in intact forest positions during summer and autumn. In gap positions soil moisture remained near 90% of field capacity during the summer months compared to 60–70% in the intact forest. Forest floor evapotranspiration did not differ between the intact forest and gap positions. Stemflow for European beech was higher than for common ash (2:1) and for both species higher when bare than when in leaf (2:1). Stemflow was highest for exposed trees when bare. On a stand level, stemflow was 2% of precipitation (in leaf), 6% (bare) and 12% (exposed trees when bare). The spatial variability in water use at the soil moisture measurement positions was correlated to tree basal area and to the distance between measurement points and the surrounding trees ($r^2 = 0.43$, $p<0.0001$). Though there was a tendency for the residuals to vary with the species dominance at the measurement positions, it was not possible to establish species specific models. High soil moisture in the gap allowed released subcanopy trees at the gap edge to sustain high rates of transpiration during the summer in contrast to trees in the stand that were limited by low soil moisture in late summer. Sap flux density was higher for released subcanopy trees than for subcanopy trees below the intact canopy in late, but not in early summer. Daily tree transpiration was higher for canopy trees than for subcanopy trees below the intact canopy during late summer and higher for canopy than for released subcanopy trees mostly in early summer. It is suggested that these changes are short lived as already in the second summer after gap establishment there were signs that the below ground gap was closing.

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The continuous emergence of relatively small canopy gaps is central to the understanding of forest succession (Runkle and Yetter 1987, Emborg et al. 2000). Resources become available to seedlings and to previously suppressed trees and especially the availability of light has been the focus of many studies (Emborg 1998, Einhorn et al. 2004, Einhorn 2007). In gaps leaves and branches are removed above ground and roots are deactivated below ground. Such a disturbance affects not only the availability of light but also the continuous exchange of water and water vapour between the soil, the vegetation and the atmosphere (the hydrological cycle, Rutter 1975). Thus, a number of important processes in the hydrological cycle are affected such as throughfall, transpiration from plants, evaporation from soil and from plant surfaces (interception loss) and seepage below the root zone. Often with the general result that soil moisture in the gap remains high during the entire growing season (Bauhus and Bartsch 1995, Gray et al. 2002, Vilhar et al. 2005, Ritter and Vesterdal 2006). The variability in soil moisture is relevant for the understanding of the nutrient- and carbon dynamics (Epron et al. 1999, 2004, Granier et al. 2003, Ritter 2007) of heterogeneous forests as well as the description and prediction of below ground competition among trees (Ammer and Wagner 2002). The available soil moisture affects the growth of seedlings (Madsen 1994, 1995, Tognetti et al. 1994). Thus the success of forest regeneration in gaps established as a means by forest management depends upon knowledge on soil moisture distribution in time as well as in space. Here, results are presented to describe the effects of a gap on the throughfall of water, on the spatial and temporal distribution of soil moisture, on the evapotranspiration from the forest floor and on the transpiration of European beech trees *Fagus sylvatica* near the gap. Further, results are shown for stemflow of European beech and common ash *Fraxinus excelsior* and some effects of crown exposure on stemflow. This study does not present calculated drainage fluxes and the water balance can therefore not be described in full. However, it presents results that are relevant when drainage fluxes are to be calculated and a suitable water balance model is to be parameterized for the site. Drainage from a forest gap to ground water reservoirs may be only marginally different from that of the intact forest; however, a calculation of fluxes for the specific stand and soil conditions in Suserup Skov is necessary to reveal this. Results from this study represent a specific point in time and space and are not suitable for a generalization across gaps. They do, nonetheless, give insight into the hydrological cycle of a forest type not often described. The high spatial resolution of the measurements is unique and the combination of tree transpiration with studies in a canopy gap has not been presented earlier.

The effect of a canopy gap on throughfall may be inferred from the observations on forest canopy interception. For European beech and oak *Quercus* sp. annual rainfall interception (% of above forest precipitation) was 33–40% in 35-yr-old stands (Thomsen et al. 2003), 25–28% for both a young and an old European beech stand and a mixed European beech-conifer forest (Granier et al. 2000a, Zirlewagen and von Wilpert 2001) and 15–36% (European beech) and 8–21% (oak) for stands of different age (Peck and Mayer 1996). Canopy interception depends on canopy structure but also strongly on rainfall intensity and duration with numerous short storms of low intensity resulting in a higher interception than few long high intensity storms (Rutter 1975). The spatial distribution of rainfall in a gap may be affected by the crown structure of the trees, which determines the amount of drip points at the crown peripheries (Linskens 1951, in Geiger et al. 1995). But it may also be affected by the wind direction and turbulence (Slavík et al. 1957, in Geiger et al. 1995). The highest values observed in the latter study (>100% of values outside the stand) were at the eastern edge (due to westerly winds) and at a few locations along the gap edges due to water dripping from the tree crowns. Values in the centre of the gap were 95–100% of values outside the stand. In the remaining locations rainfall approached the level observed in the stand. Gaps are dynamic in nature and the ground vegetation may grow fast during the first few years after the formation of the gap (Ritter et al. 2005). Thus, rain may fall directly on the soil (net-precipitation) immediately after gap formation. As the ground vegetation develops some of the rain is withheld as interception loss and unless rain collectors are placed at the ground level this loss is not included in the measurements.

The amount of rain reaching the soil as stemflow tends to be species specific. In a review Levia and Frost (2003) collected evidence of the importance of bark texture. Smaller amounts of stemflow were found in species with rough or flaky bark than in species with smooth bark because of differences in water storage capacity. Branch inclination, angle and crown geometry as well as individual tree size and exposure were also found to be determinants with high inclination angles, large trees and exposed crowns giving high stemflow values. Annual stemflow in European beech (smooth bark) was 4% of precipitation (Neal et al. 1993) with less in the growing season than in the dormant season and 5% of precipitation in the growing season (Granier et al. 2000a). Annual stemflow was up to 20% of precipitation for European beech (Ladekarl 2001 and references therein). In contrast stemflow in oak (rough bark) was < 2% of precipitation (Nizinsky and Saugier 1988, in Ladekarl 2001). Common ash is expected to have less stemflow than European beech because of a coarser bark texture.

While the formation of a canopy gap leads to increased light availability to previously overtopped vegetation with a spatial distribution governed by solar inclination and altitude as well as stand structure (Canham et al. 1990, Ritter et al. 2005) the soil moisture response may be less predictable. Slavík et al. (1957, in Geiger et al. 1995) found, in a mixed oak-European beech forest, that soil moisture in the

central part of a small (diameter <20 m) gap remained high during the entire summer. Soil moisture in the topsoil of small gaps also remained high throughout the growing season in European beech (Bauhus and Bartsch 1995), tropical wet forest (Ostertag 1998) and coastal Douglas-fir *Pseudotsuga menziesii* (diameter 0.2–1 × stand height) (Gray et al. 2002). The latter study found that soil water content generally was higher in the deep soil layer (15–45 cm) than in the topsoil, that intermediate size gaps (diameter near 0.5 × stand height) showed a more pronounced soil moisture response than small (diameter 0.2 × stand height) and large (diameter 1 × stand height) gaps and that soil moisture was lower at the northern than at the southern gap edge of large gaps due to direct radiation and high evapotranspiration. They further concluded that, although there was a general tendency for gap centers to show high soil moisture, radiation and variability in soil humus content created dry micro sites for seedlings also in the centre of gaps. Similarly, gap formation in a *Nothofagus pumilio* forest created both dry and moist conditions in the topsoil (Heinemann et al. 2000). Where understorey vegetation grows to dominate the gap a soil moisture response may not be observed at all (McGuire et al. 2001). Clearly, the growth and survival of seedlings and the distribution of other vegetation in a gap as well as the nutrient cycle and soil fauna may be affected by the soil moisture distribution (Ritter 2007, Bjørnlund and Lekfeldt 2007, Hahn et al. 2007). The gap effect for soil moisture disappears with time. In a temperate coniferous forest after ca 4 yr (Gray et al. 2002) and after 1 yr in a tropical forest (Veenendaal et al. 1995). The duration of a gap effect for soil moisture is closely related to root distribution and root expansion (Brockway and Outcalt 1998, Ammer and Wagner 2002, Müller and Wagner 2003). However, root distribution is difficult to measure; therefore it is attractive to be able to predict root distribution from the vegetation. The relationship between root and single-tree distribution has been investigated for European beech (Nielsen and Mackenthun 1991) and Norway spruce *Picea abies* (Ammer and Wagner 2002). For both species fine root density decreased with distance to the tree in a nonlinear way and at some sites it increase with tree basal area. Such models have so far not been applied in mixed heterogeneous stands to describe the activity of roots (i.e. water extraction).

The fact that root gaps do not last forever implies that some trees benefit from the high soil moisture found in gaps in their early stage. During the growing season the water content of the forest soil generally declines due to the combined effects of interception loss and transpiration. During dry periods, often in early autumn, the stand is subject to mild or severe water stress (Granier et al. 2000a, b). High soil moisture after gap formation may allow trees near the gap to sustain high transpiration rates in periods where trees in the stand experience beginning (or severe) water stress. Thus the release of trees following the formation of a canopy gap may not refer exclusively to the availability of light, but also to the access to soil water. In Scots pine *Pinus sylvestris* edge trees were observed to have higher transpiration than trees in the stand (Cienciala et al. 2002). As photosynthesis and transpiration rates are proportional (Catovsky et al. 2002) this would imply, that the growth of trees near a canopy gap and the closure rate of gaps depends on the available soil water.

In closed forests the evapotranspiration from the forest floor in the growing season is low – usually below 10% of stand evapotranspiration (Granier et al. 2000a, Wilson et al. 2000). However, the periodic contribution can be up to 20% of total stand evapotranspiration (Kelliher et al. 1992) and for a vegetated forest floor above 50% (Roberts et al. 1980). Evaporation near the forest floor was higher in the northern than the southern part of a canopy gap (Slavík et al. 1957, in Geiger et al. 1995), but measurements contrasting gap and intact forest conditions have not been presented. However, in references given above (Heinemann et al. 2000, Gray et al. 2002) it is evident that the topsoil in gaps has been observed to become dry implying some evaporation in these gaps from the upper soil layers. A dry topsoil (0–15 cm) does not contradict the existence of deeper soil layers with high soil moisture (as found by Gray et al. 2002), but it triggers the question if forest floor evaporation is higher in a gap than below the intact forest canopy.

The basic hypothesis of this study is: 1) following the creation of a canopy gap, soil moisture in the gap is higher than below the intact forest canopy. Input and output of water were subject to individual investigations based on the following hypotheses: 2) throughfall in the canopy gap is higher than below the intact forest canopy. 3) Stemflow depends on species (European beech > common ash) and is higher for exposed trees than for trees in the closed stand. 4) Water uptake from the soil (water use) is related to the position and the size of trees near the gap; thus, the extent of a root gap can be predicted from tree size and position. 5) Evapotranspiration from the forest floor is higher in the gap than below the intact forest canopy. 6) Tree transpiration rates depend on tree position relative to the canopy gap with the highest transpiration rates found for trees near the canopy gap.

Methods

Measurement site

The site is in Suserup Skov, a 19.2 ha uneven-aged mixed deciduous forest (55°22′N, 11°34′E), where a 20-m diameter gap was formed in the storm of December 1999 (Ritter et al. 2005, Heilmann-Clausen et al. 2007). The gap is very irregularly shaped. It was formed when a large old canopy tree lost most of its crown and a number of smaller trees were windthrown. Along the gap edges several

small trees were released by the formation of the gap. The soil is a loamy till with pockets of sandy till (inceptisol) developed from moraine deposits (Vejre and Emborg 1996). The measurement plot was on a well-drained plateau in the central part of the forest. The groundwater level was below 1.2 m throughout the year based on the lack of gley-characteristics in the soil profile (Ritter and Vesterdal 2006). The plot was northeast of a lake (Tystrup Sø) and 80 m from the northern forest edge bordering agricultural fields. Stand basal area at the measurement plot (based on measurements in a 6400 m^2 area around the gap) was 40.2 m^2 ha^{-1}. Total tree density (diameter > 4.5 cm) was 733 stems ha^{-1}. Four tree species were present near the gap; percentage of basal area is given below: European beech 56.1%, common ash 28.1%, wych elm *Ulmus glabra* 2.8% and pedunculate oak *Quercus robur* 13.1%. Across all trees mean tree height was 13.3 m and stand top height was 28.4 m. The mean diameter was 18.5 cm, 1st quartile for diameter was 6.8 cm and 3rd quartile was 22.3 cm. The stand is also characterized by a number of large old trees (European beech and pedunculate oak) reaching diameters near 150 cm. Tree positions, tree heights and diameter were determined in January 2000, supplemented by measurements in 2001–2002 (Brunner, Dalsgaard, Einhorn and Ritter unpubl.). The oldest European beech trees have been dated to almost 300 yr and the structure now resembles that of a natural forest (Emborg et al. 1996, 2000).

Meteorological measurements

Precipitation (P; Pronamic, Rain-o-matic, area 0.02 m^2, resolution 0.2 mm), air temperature and relative air humidity (Vaisala HMP45A), solar radiation (Li-Cor LI190SA Quantum Sensor) and wind speed (Vector Instruments A100L2, cup anemometer) was measured 2 m above the ground in a field 300 m from the stand edge. P was corrected for wetting (evaporation directly from the funnel surface) and for the influence of turbulence near the funnel (Vejen et al. 2000). Corrections are based on on-site meteorological measurements in the height of the funnel (2 m) and assuming that the daily wetting is the same for 2 m as for the height used by the Danish Meteorological Inst. (1.5 m). Air temperature and relative air humidity at 2 m was also measured in the stand near the gap using the same type of instruments. Instruments were scanned every 10 s and observations were averaged every 30 min. Air vapor pressure deficit (D) was calculated from measurements of air temperature and relative air humidity.

Measurement positions for throughfall and soil moisture

Measurements were placed in an 8 × 8 point grid covering the gap with 6 m between positions in the north-south direction and 5 m between positions in the east-west direction. Fifty-nine of the 64 positions were equipped with instruments. The distances between positions as well as the total number stem from the need to coordinate measurements among researchers working at the site and in the same gap. Until 19 April 2001 all 59 positions were measured. After this day 28 of the 59 positions were measured (Fig. 5d, see caption). The positions were divided into three categories: intact forest (29/10): positions below the main canopy and 2 m from the stem of trees bordering the gap (in the direction away from the gap); gap (13/10): positions in open conditions and 2–3 m from the stem of trees bordering the gap (in the direction toward the gap); edge (17/8): remaining positions. The number of observations in each category is given in brackets (before/after 19 April 2001).

Throughfall and stemflow

Throughfall (TF) was measured manually with a weekly-monthly resolution using plastic funnels (diameter 11.8 cm) placed 1 m above the ground (and above the ground vegetation for all measurement positions). In the central part of the gap, throughfall may be equal to the precipitation. However, acknowledging that rain falling in a small canopy gap may be affected by the surrounding tall canopy the term "throughfall" was chosen. This allows for the same terminology for positions in the intact forest as well as in edge and gap positions. The water collected in the funnels was led into bottles buried in the ground. Measurements were corrected for wetting (Vejen et al. 2000).

Stemflow (SF) was measured on 10 trees (five common ash 17–50 cm diameter and five European beech 14–57 cm diameter). Two were at the edge of a small opening near the investigated canopy gap thus with exposed crowns. The remaining trees were in the stand near the investigated gap. None of the trees were near the soil moisture measurement positions. On each tree a profile silicon collar was spiralled twice around the stem 1.5 m above the ground. The water was led to a container (with a known volume) beside the tree and the amount of water in the container was measured manually once a week (May–October) or approximately once a month (November–April).

Soil moisture

The volumetric soil water content (SWC, vol.%) was measured by Time Domain Reflectometry (Topp et al. 1980, Thomsen 1994) (Tektronix 1502C/1502B). Measurements were at the positions described above. Probes were stationary and integrated over a 0.3, 0.5 or 0.9 m soil profile and consisted of two 6 mm stainless steel rods. Measurements were manual and bi-weekly (May–October) or monthly (November–April). The soil water con-

tent measured with TDR in vertical profiles was within 15% of the gravimetrically determined values (February 2001) scaled to a soil profile (n=3 for each of four horizons). For analyses of tree transpiration only measurements from below the intact forest canopy were used (depth 0.5 m, n=10). These can be expressed as the available soil water ((SWC-WP)/FC-WP), where WP is wilting point and FC is field capacity. Field capacity was found as the mean of measurements from 25 January to 24 April (for some positions 19 April). During this period SWC measurements were stable and for the 0–0.9 m and 0–0.5 m probes within 5% of the mean value (FC) for each position except for one in 0–0.5 m (within 5.3% of FC). In 0–0.3 m depth SWC was within 10% of the mean value (FC) except for one position (within 21.5% of FC). The mean value (and not the maximum) was used to avoid a very high FC due to recent rain or slow drainage of water from the soil. The mean in-situ FC was 229 mm (0–0.9 m), 134 mm (0–0.5 m) and 89 mm (0–0.3 m). Soil water retention was determined in the laboratory on soil samples from two soil profiles (n=4 or n=8 for each horizon) (Schønning 1985). Calculated field capacity for the two soil profiles based on the water content at –0.01 MPa (pF 2) were 5–12% lower than the values measured in-situ: 202 mm (0–0.9 m), 127 mm (0–0.5 m) and 81 mm (0–0.3 m). Wilting point (WP) in 0–0.5 and 0–0.9 m was calculated from laboratory samples (–1.5 MPa, pF 4.2) to 4.4 and 4.3 vol.% respectively (22 and 39 mm). The two profiles were in the intact forest north-east and north-west of the gap. Due to the protected status of the forest as well as a lack of space in the gap area it was not possible to obtain soil water retention data from the gap or the edge.

Transpiration

Sap flux density (J_s, g m^{-2} s^{-1}) was measured using the thermal dissipation technique (Granier 1985, 1987, Granier et al. 1996). J_s was measured on 12 European beech trees from 15 June to 30 September 2000 (Dalsgaard unpubl.). The sample trees (diameters 0.11–0.70 m) were positioned north-west of the gap; some in the intact forest and some in the gap edge. Averages were logged every 30 min and J_s was calculated using the calibration formula developed by Granier (1985). Probes (one pair per tree) were inserted radially into the northern side of the stem 2 m above the ground with a vertical distance of 0.2 m and protected from rain and from direct sunlight. Measurements were scaled from sensor to tree by using a model for the radial variation in sap flux density: relative $J_s = 1.0075/(1 + (x / 4.8896)^{3.0836})$, where x is the depth (cm) and the relative J_s is J_s at a given depth relative to J_s measured in the outer 20 mm of the xylem (Dalsgaard unpubl.). The model was based on measurements from Suserup Skov and predicts a decreasing J_s with increasing xylem depth as also found by other authors (Köstner et al. 1998, Lang 1999, Granier et al. 2000a). Tree transpiration was the tree scaled sap flux density related to the crown projection area.

Forest floor evapotranspiration

Evapotranspiration and soil evaporation from the forest floor was measured with small lysimeters (depth 150 mm, diameter 85 mm) at two occasions: 14–15 August 2001 (1 d) and 29–31 August 2001 (2 d). At each occasion 16 lysimeters were placed in the intact forest and gap locations. Half of the lysimeters included small seedlings (mean seedling height at the two occasions was 26.4 and 27.0 cm (gap) and 20.1 and 24.3 cm (intact forest)). The other half of the lysimeters included only soil and litter. Evaporation was determined as the difference in weight (g, two decimal points) in the morning on subsequent days. No rain occurred during the measurement periods.

Statistical analyses

For throughfall (TF) differences among gap, edge and intact forest positions (Tukey-Kramer adjusted t-test, $p<0.05$, PROC GLM, SAS 8.2) were tested for spring (April–May), summer (June–September), autumn (October–November) and winter (December–March). Data were available from June 2000–January 2002 giving a total of seven periods. For each period throughfall was summed for each measurement position. Positions N, S, E or W of the gap centre were compared using the 45°, 135°, 225° and 315° angles as dividing lines between groups. Positions NE, NW, SE or SW of the gap centre were compared using the 90°, 180°, 270° and 360° angles as the dividing lines. Data were used from both the grid (59 positions) and transect (28 positions).

The mean throughfall within each category was regressed on precipitation (bi-weekly to monthly measurements). The effects of category and season (defined as above) across all data was found by testing the significance of their interaction with P. For each season the effect of the interaction between P and category was tested. For each category the effect of the interaction between P and season was tested. The effect of year was found for measurements in summer (2000/2001) by testing the significance of the main effect as well as the interaction with P. Regressions ($Y=\text{slope} \times P$) are presented for specific seasons and categories. PROC GLM, SAS 8.2 was used for all tests and regressions. Data were used from 28 positions measured in June 2000 through August 2001 (P was not measured after this date).

For each tree stemflow (SF) was regressed on P and the significance of season was tested. Observations 1 November–3 May were categorized as bare (winter) and remaining observations as in leaf (summer). The funnelling ratio (Herwitz 1986 in Levia and Frost 2003, Herwitz and Levia

1997) for individual trees F = V/BA·P is given for selected periods (V is stemflow volume, BA is tree basal area). Subsets of the data were excluded from the analyses due to plugging or overflow from the containers. Further, for each season and for each of SF and SF/BA, the significance of tree basal area, species (ash, beech) and crown exposure (edge, stand) was tested in one model incorporating P as well as stemflow from all trees. PROC GLM, SAS 8.2 was used for all tests and regressions. Species specific models for SF/BA are used to predict the stand stemflow from P. The response (SF in L period^{-1} or SF/BA in L m^{-2} period^{-1}) was transformed when necessary to obtain homogeneity of variances. Transformations used were a log transformation: Y=ln(SF+1) and the Freeman-Tukey transformation:Y=(SF/BA)$^{0.5}$ + (SF/BA+1)$^{0.5}$ (Weisberg 1985).

For soil moisture, differences among gap, edge and intact forest positions were tested (Tukey-Kramer-adjusted t-test, p<0.05, PROC GLM, SAS 8.2). Response variables were SWC in 0–0.3 m depth (SWC_{30}) and in 0–0.9 m depth (SWC_{90}) and the relative SWC in the two depths ($RSWC_{30}$ and $RSWC_{90}$), which is SWC as a fraction of field capacity. Data were used from both the grid (59 positions) and transect (28 positions). All responses were averaged over periods ranging from 1 to 4 months: spring: mid April–May, summer: June–September, autumn: October–December (autumn 2001 measured only in October), winter: January–mid April. Measurements were available from June 2000 to October 2001 giving a total of six periods. An effect of position relative to the gap centre was tested as described above for throughfall.

To relate tree position and soil water dynamics periodic water use was calculated in 0–0.5 m depth (WU_{50}) and in 0–0.9 m depth (WU_{90}). Five summer periods in 2000 were identified where for each period P<1 mm. They were: 16–20 June, 3–7 July, 11–18 July, 25–28 July, and 4–8 August. The observed changes in soil water content were assumed to be caused primarily by water uptake by tree roots. For WU_{50} the four periods were selected that had the highest SWC (period 1, 2, 3, and 5). SWC in 0–0.5 m depth was 14.8–19.4 vol.% in intact forest positions and 22.9–27.0 vol.% in gap position during these periods. For WU_{90} period 2, 3 and 4 were selected. For each position the changes during the relevant periods were summed (= water use in vol.%). A nonlinear model (Nielsen and Mackenthun 1991) relating water use at each position to tree position and basal area of the 20 closest trees was parameterized using PROC NLIN (SAS 8.2).

$$\text{water use} = \sum_{i=1}^{i=20} \frac{a \times BA_i^d}{1 + b \times \exp(c \times dist_i)} \quad (1)$$

Where BA_i is stem basal area of $tree_i$ (m^2), $dist_i$ is the distance (m) between the position and $tree_i$ and a, b, c and d are fitted parameters. Dead trees were not included and the old tree/stump in the centre of the gap (the gap maker, Fig. 2d) was also left out though a small part of the crown still remained. A total of 197 trees entered the model (for each TDR position the 20 closest trees thus some trees more than once). 70% were European beech, 13% were common ash and the rest pedunculate oak (one old tree) and wych elm (numerous small trees). Possible differences in water use among tree species were investigated in the following two ways: 1) for each of WU_{50} and WU_{90}, eq. 1 was allowed to have specific parameters for European beech and for the remaining species, thus, a total of 8 parameters; 2) for each position the basal area of each species (relative to the total basal area) for the closest 20, 10 or 5 trees was related to the studentized residuals found from eq. 1 (common parameters for all species).

Differences between gap and intact forest positions on forest floor evapotranspiration was tested (Tukey-test, $p < 0.05$; PROC GLM SAS 8.2) for each of three observation periods and for the sum of the two observations on 29–31 August.

The effect of tree size and position on tree transpiration was investigated by identifying three groups of trees (Dalsgaard unpubl.): canopy trees (can: height > 20 m; n=6(5)), subcanopy trees below the intact canopy (sub_F: height < 20 m; n=3), subcanopy trees in the edge of the canopy gap (sub_O: height < 20 m; n=3). Differences (t-test, PROC GLM SAS 8.2) in mean and maximum sap flow rates were tested in a monthly resolution (J_{s-sum} (kg water m^{-2} sapwood d^{-1}; and J_{s-max} (kg water m^{-2} sapwood half-hour^{-1})). Differences in the daily transpiration rates were tested in a weekly resolution (E_{sum} (mm d^{-1}). The daily sap flux density for can and sub_F relative to sub_O (in %) was analyzed in a multiple linear regression with daily values of global radiation, vapour pressure deficit and available soil water in 0–0.5 m.

Results

Weather during the measurement period

The summer of 2000 was relatively cool with frequent rain episodes whereas the summer in 2001 was warm. In 2000 mean air temperature (°C) measured on site for July, August and September were 15.4, 15.7 and 13.2. In 2001 the mean air temperature in July and August were 17.9 and 17.2. Precipitation was low in July for both years, but August was dry in 2000 and wet in 2001. Soil water content in 0–0.9 m in the intact forest reached a low of 11.5 vol.% (103.7 mm) in early September 2000 and 11.0 vol.% (99.1 mm) in early August 2001 (Fig. 1).

The spatial pattern of throughfall

Throughfall in the intact forest positions was significantly lower than in gap positions in summer and in spring (Table 1; 77–84% of throughfall in the gap), but edge posi-

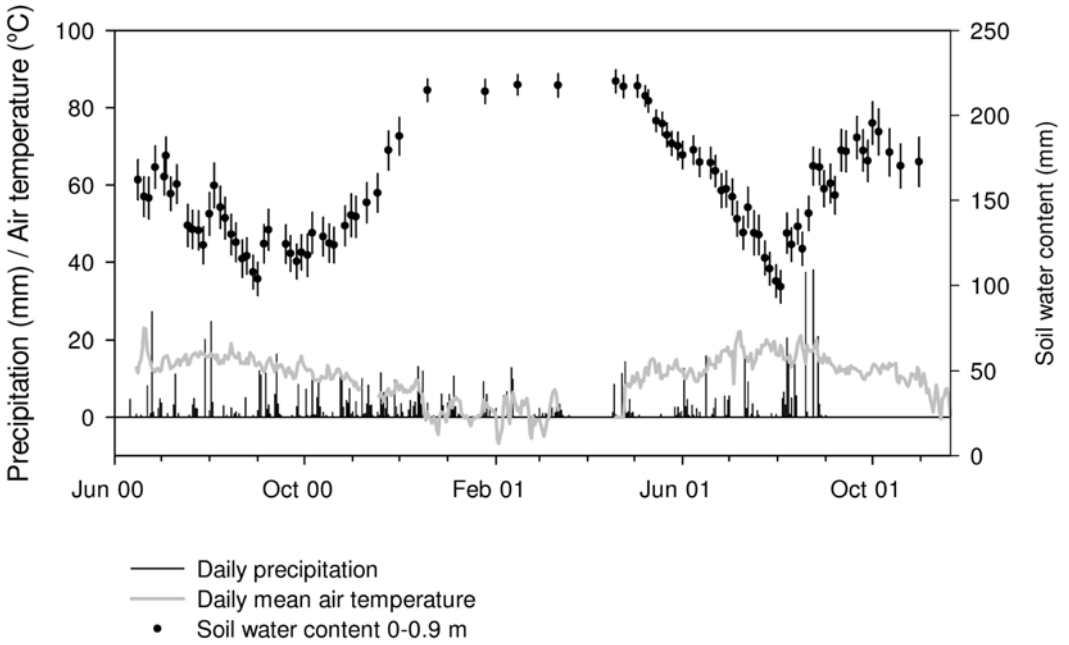

Fig. 1. Air temperature, precipitation and soil moisture in the intact forest (0–0.9 m) June 2000–October 2001 in Suserup Skov. For technical reasons the measurement of precipitation stopped in September 2001. The lack of meteorological measurements in early spring 2001 is due to the maintenance and calibration of equipment. Error bars show ± one standard error of the mean.

tions were never different from the intact forest. Similarly, annual and total throughfall was lower in the edge and intact forest positions than in the gap. In autumn positions north of the gap centre received more throughfall than positions east and south of the gap centre (114 vs 98 and 96 mm; 2000) or positions west of the gap centre (128 vs 105 mm; 2001). The interaction between category and orientation relative to the gap centre was never significant.

Regression of throughfall on P showed that across years the interaction with both category ($p<0.001$) and season ($p=0.0009$) were significant ($r^2=0.97$). Throughfall relative to P in summer was higher in 2000 than in 2001 ($p<0.0001$; Fig. 2). Throughfall depended on category only in summer, with up to 99% of P in the gap in 2000 and down to 71% in edge positions in 2001 (Fig. 2). Across years and for gap positions the interactions between P and season was significant ($p=0.03$) with throughfall up to 92% of P in summer and down to 76% in autumn (Fig. 3). Across all data there was no significant difference between edge and intact forest positions. For edge and intact forest positions throughfall depended on season ($p=0.003$) with up to 80% of P in winter and down to 68% in autumn. Summer canopy storage capacity was estimated for the intact forest to 1.20 mm (equation: $Y= -1.20 + 0.783 \times P$; $r^2=0.95$).

Stemflow

Data showed a large variability in stemflow volumes (SF) and there were clear effects of season, species, BA, and crown exposure. The regressions of stemflow on precipitation for the individual trees gave r^2-values of 0.51–0.79 for trees in leaf and 0.57–0.83 when bare. For all trees except one, season was significant ($p<0.05$) (Table 2). Funneling ratios were 0.9–3.3 and 8.6–18.9 for common ash and 5.1–8.4 and 15.4–47.0 for European beech (in leaf and bare respectively, Table 2). During a summer period where measurements for the exposed crowns were missing (29 May–24 July 2001) funnelling ratios were 1.2–2.6 for common ash and 3.3–6.4 for European beech. Across all trees SF was predicted from P, BA, exposure and species (bare: $p<0.0007$ for all effects, r^2-value 0.74; in leaf: $p<0.0001$ for P, species and BA, r^2-value 0.62). For the summer a model including interaction effects: P ($p<0.0001$), P × species ($p<0.0001$), P × BA ($p<0.0001$), exposure (ns) yielded a slightly higher r^2-value of 0.69. To determine the mode of up-scaling SF/BA was analyzed relative to stand structure. Across all trees SF/BA was predicted from P, BA, exposure and species (bare: $p<0.0001$ for P, exposure and species, r^2-value 0.71; in leaf: $p<0.0001$ for P and species, r^2-value 0.68; BA ns in both cases). When using the P × species interactions in-

Table 1. Mean throughfall in the intact forest, edge and gap in Suserup Skov, Denmark, June 2000–January 2002. Different letters indicate significant ($p<0.05$) differences using the Tukey-Kramer adjustment for multiple comparisons. SE is the standard error of the mean. June 2000–April 2001 all 59 positions in the grid were used and values in the square brackets are based on the 28 positions measured throughout all of seven periods. April 2001–January 2002 n=28. Canopy interception (not including stemflow: ((P – throughfall)/P) for some of the periods is also shown.

Time period	Throughfall mm (SE) *Canopy interception % (SE)* Intact forest	Gap	Edge
June–September 2000	^{A}179.5 (6.3) [^{a}171.0 (5.6)] *21.7 (2.8)[25.4 (2.5)]*	^{B}213.2 (8.4) [^{b}220.1 (8.2)] *7.0 (3.7) [4.0 (3.6)]*	^{A}181.7 (6.8) [^{a}178.3 (12.5)] *20.7 (3.0) [22.2 (5.5)]*
October–November 2000	^{A}101.8 (2.5) [^{a}99.5 (6.1)] *32.3 (1.6) [33.8 (4.1)]*	^{A}108.4 (5.8) [^{a}112.2 (6.09)] *27.9 (3.9) [25.4 (4.0)]*	^{A}107.8 (4.2) [^{a}103.0 (6.5)] *28.3 (2.8) [31.5 (4.3)]*
[1]December 2000–19 April 2001	^{A}176.9 (2.8) [^{a}175.7 (6.4)] *20.1 (1.3) [20.5 (2.9)]*	^{A}175.0 (5.4) [^{a}180.3 (3.6)] *22.1 (2.7) [19.7(2.0)]*	^{A}183.1 (4.5) [^{a}179.1 (4.3)] *17.8 (2.3) [20.0 (2.2)]*
[1]24 April–May 2001	^{A}37.7 (1.2) *29.2 (2.6)*	^{B}44.9 (1.2) *22.3 (1.1)*	^{A}39.5 (1.2) *28.9 (2.5)*
[1]June–September 2001	^{A}267.6 (12.0) *29.9 (3.8)*	^{B}348.5 (12.8) *10.6 (3.1)*	^{A}273.1 (16.4) *30.3 (4.4)*
October–November 2001	^{A}108.0 (5.8) –	^{A}121.6 (7.0) –	^{A}114.4 (4.0) –
December 2001–January 2002	175.7 (8.8) –	163.6 (5.5) –	181.4 (3.0) –
Total integrated	^{A}1035.1 (32.5) *27.5 (2.4)*	^{B}1191.3 (27.7) *13.8 (2.0)*	^{A}1068.9 (32.1) *26.2 (3.0)*
Annual: 27 June 2000–26 June 2001	^{A}515.6 (15.2) *27.5 (2.2)*	^{B}603.2 (13.0) *15.2 (1.8)*	^{A}533.0 (19.4) *25.4 (3.0)*

[1]Canopy interception does not cover exactly the same interval as throughfall because of missing data for precipitation.

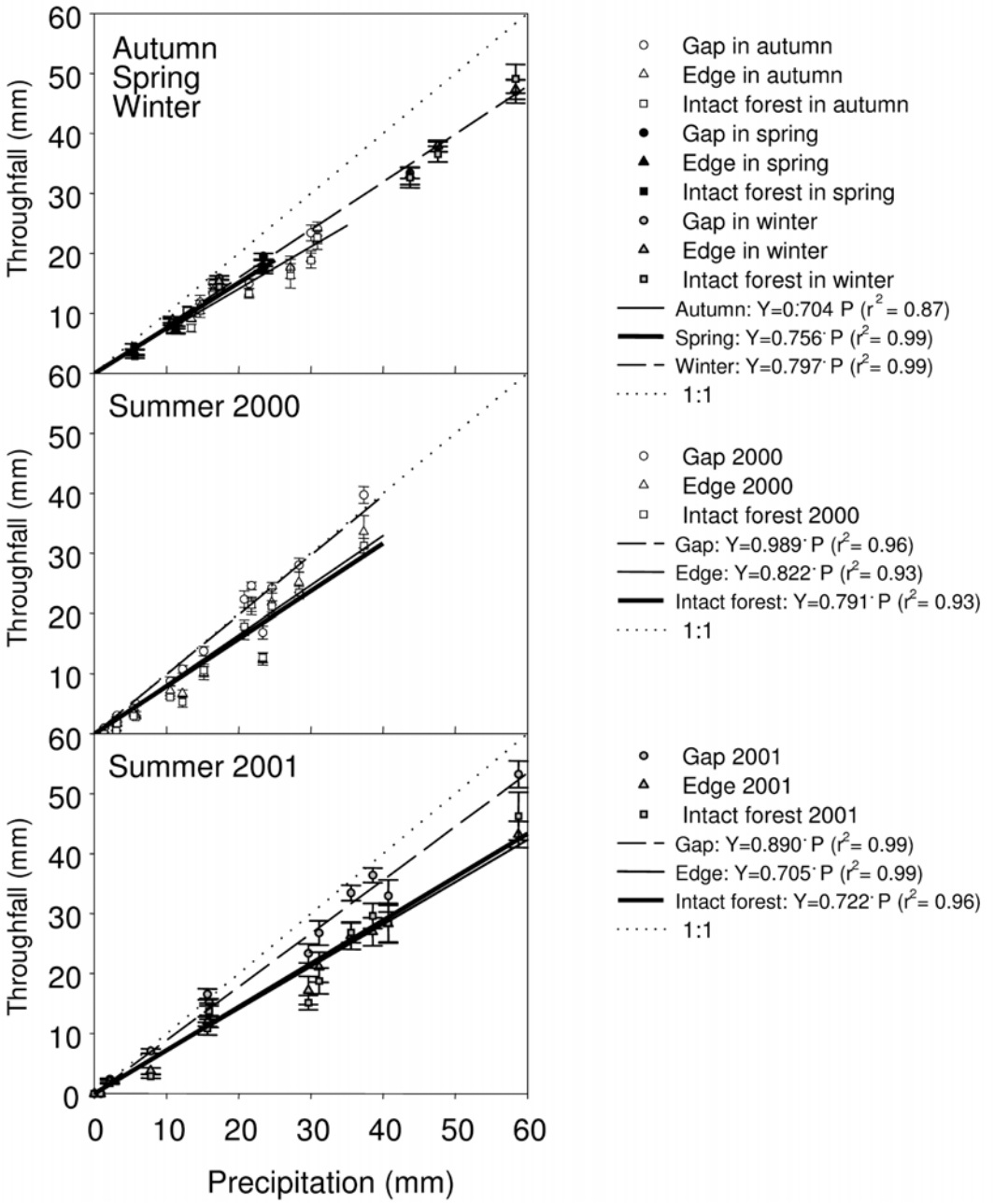

Fig. 2. Throughfall relative to precipitation in gap, edge and intact forest position in Suserup Skov. Difference among categories were significant only during the summer. Error bars show ± one standard error of the mean.

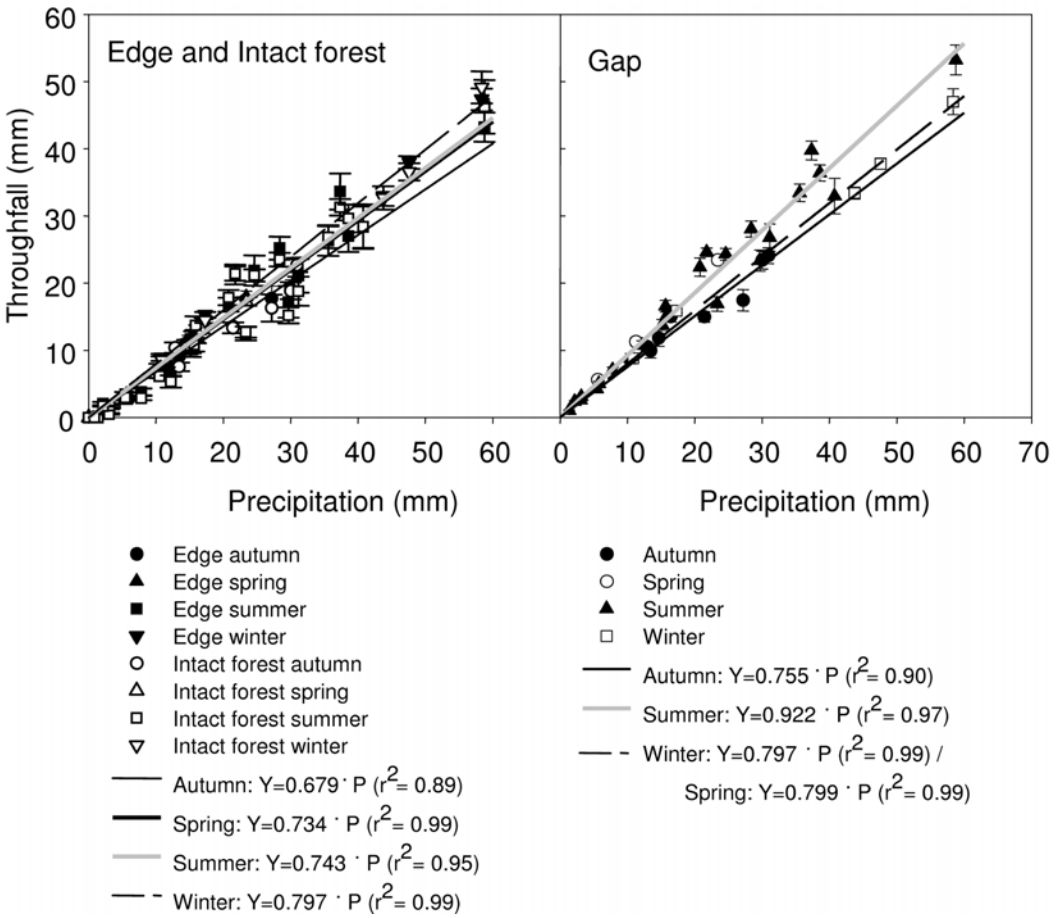

Fig. 3. Throughfall relative to precipitation for different seasons in Suserup Skov. Across seasons there was no significant difference between the edge and intact forest positions. In gap positions the regressions for winter and spring were almost identical and both are represented by the broken line. Error bars show ± one standard error of the mean.

stead of the species effect results were for the winter (r^2-value 0.71): P ($p<0.0001$), P × species ($p<0.0001$), BA (ns), exposure ($p<0.0001$); and for the summer (r^2-value 0.71): P ($p<0.0001$), P × species ($p<0.0001$), BA (ns), exposure (ns). Stemflow was scaled to the stand level using the cumulated BA of common ash (11.7 m^2 ha^{-1}) and European beech (22.5 m^2 ha^{-1}). Regressions for SF/BA on P for each species, season and exposure (r^2-value 0.59–0.76) as well as stemflow scaled to stand level are shown in Fig. 4. Stemflow was transformed (Freeman-Tukey) and curves show the back-transformed values. Based on the predicted stemflow scaled to the stand level stemflow was 2.2% of precipitation when in leaf, 6.0 % in the closed stand when bare and 12.2% for exposed trees when bare.

The spatial pattern of soil moisture

Field capacity (FC) varied across positions, but for the 0–0.9 m depth there was no significant difference among categories and the mean FC was 229 mm (standard error of the mean: 0.5 mm) For 0–0.3 and 0–0.5 m FC in edge positions (93 and 141 mm) were significantly higher ($p<0.05$) than in the intact forest (86 and 130 mm) and FC in the gap was intermediate (92 and 136 mm). There were no indications that FC was higher close to tree stems thus any effect on FC of stemflow did not emerge. However, only in eight occasions was the soil moisture measurement within 1 m of tree stems. Differences among categories emerged during the summer and autumn (Fig. 5) with

Table 2. Stemflow for individual trees predicted from precipitation. The level of significance (p-value) of season is shown as well as stem diameters and regressions for each tree when bare and when in leaf. Observed stemflow and funneling ratio (see text) are shown for selected periods. Trees #9 and #10 were at the edge of a small opening and their crowns were exposed.

#	diam. (cm)	in leaf [c]regression (n) r^2	bare regression (n) r^2	[c]p<value	Stemflow $L \times tree^{-1}$ (funneling ratio) [a]in leaf P=134 mm	[b]bare P=193 mm
Common ash *Fraxinus excelsior*						
1	24.2	y_t=0.045+0.034x (34) 0.51	–	–	5.3 (0.9)	–
2	49.7	y_t =0.082+0.085x (30) 0.63	–	–	69.3 (2.7)	–
5	16.9	y_t =0.028+0.035x (21) 0.56	y=–1.843+0.322x (12) 0.57	0.0001	6.4 (2.1)	40.6 (9.4)
6	28.3	y_t =0.152+0.065x (21) 0.63	y=–14.732+1.336x (12) 0.62	0.1742	28.2 (3.3)	105.0 (8.6)
10	38.2	y_t =0.044+0.085x (7) 0.63	y=–6.523+2.438x (8) 0.68	0.0008	48.3 (3.1)	419.0 (18.9)
European beech *Fagus sylvatica*						
3	57.3	y_t =–0.045+0.19x–0.002x^2 (30) 0.78	y=–40.710+6.268x (11) 0.77	0.0019	223.6 (6.5)	778.9 (15.6)
4	32.8	y_t =–0.045+0.148x–0.001x^2 (30) 0.79	y=–45.553+4.405x (12) 0.78	0.0035	93.3 (8.4)	422.1 (25.9)
8	14.3	y_t =0.190+0.040x (21) 0.57	y=–1.757+0.413x (12) 0.62	0.0023	11.1 (5.1)	48.0 (15.4)
9	36.3	–	y=–25.731+5.928x (8) 0.83	–	–	939.7 (47.0)

[a] 12 September–31 October 2000.
[b] 10 November 2000–25 January 2001.
[c] The response was transformed: y_t = ln(stemflow+1).

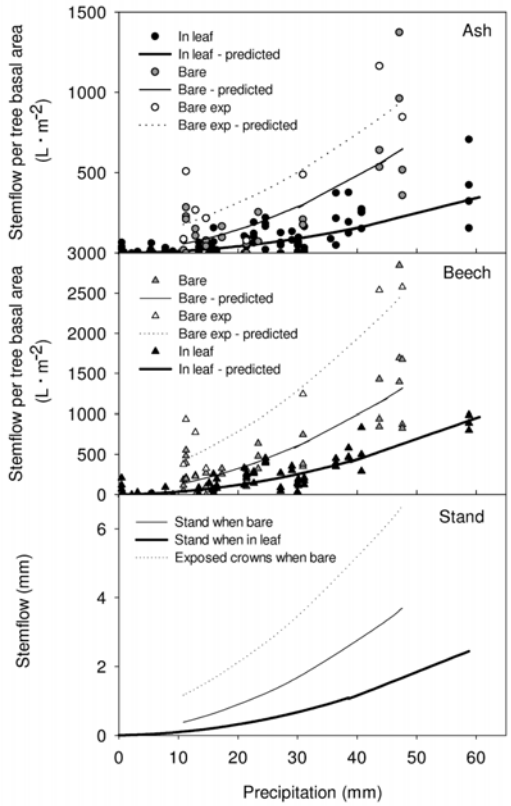

Fig. 4. Stemflow relative to precipitation ($L \times m^{-2}$ tree basal area) for common ash *Fraxinus excelsior* and European beech *Fagus sylvatica* and total stand stemflow (mm) relative to precipitation in Suserup Skov, Denmark. Curves for exposed conditions scaled to the stand level use the same distribution of basal are to the two species as in the closed stand (see text). Data were obtained June 2000–August 2001 and each observation cover 1-several precipitation events. Curves show the back-transformed predictions using the Freeman-Tukey transformation ($(stemflow)^{0.5} + (stemflow+1)^{0.5}$). R^2-values for ash (predictions) were 0.59 (bare), 0.61 (bare exposed) and 0.59 (in leaf). For beech they were: 0.67 (bare) 0.76 (exposed) and 0.75 (in leaf).

gap positions showing higher soil moisture than positions in the edge and in the intact forest.

For both 0–0.3 m and 0–0.9 m there was a clear soil moisture effect of the gap. In summer and autumn SWC was generally higher in gap positions, intermediate in edge positions and lowest in the intact forest (Table 3). Edge occasionally differed from gap and intact forest positions in summer and autumn, but not in all cases. In winter intact forest SWC was slightly lower than in gap and edge positions. I spring intact forest and gap positions differed. RSWC showed the general result that edge positions were different from both gap and intact forest positions until autumn 2000. In 2001 edge was not different from the intact forest positions. Positions to the north were never significantly drier than other positions, neither for the entire measurement area nor for positions within the gap. Rather it was revealed that southern and southeastern positions in the measurement area were generally drier than other positions. This was most pronounced for the SWC and less pronounced for RSWC indicating that the relative values may express better the differences between the gap, edge and the intact forest.

Soil moisture dynamics and the correlation to tree position

For water use (WU), WU_{50} was 5.0–15.3 vol.% (the equivalent of 24.9–76.5 mm during 19 d) and WU_{90} was 1.8–6.7 vol.% (the equivalent of 16.2–60.3 mm during 14 d). Predicted and observed values of water use are shown in Fig. 6a, the regressions were both tested to be significant ($p<0.0001$). Predicted water use for each position increased with decreasing distance to trees (Fig. 6b) and increased with tree basal area (Fig. 6c). In two periods with SWC in 0–0.5 m depth below 14.8 vol.% (25–28 July and 25–29 August) predicted and observed values of WU_{50} showed very poor correlation as expected. For comparison water use in 0–0.9 m depth was calculated for the same periods as those used in WU_{50}, however, the fitted model ($r^2=0.29$) was further from the 1:1 line than those shown in Fig. 6a (predicted water use (mm d^{-1}) = $1.7+0.31 \times$ observed water use). It was not possible to establish species specific models for either WU_{50} or WU_{90}. When relating the basal area for each species to the studentized residuals from eq. 1 (WU_{50}) the most extreme studentized residuals (high and low) were found for positions with a medium or high relative contribution of common ash to the total basal area for the 5, 10 or 20 closest trees. A similar analysis for WU_{90} showed that studentized residuals increased with increasing common ash dominance and decreased with increasing European beech dominance. For the closest 20 trees studentized residuals significantly depended on ash dominance ($p=0.03$).

Forest floor evapotranspiration

Daily soil evaporation was lower than daily evapotranspiration including vegetation, but differences between intact forest and gap positions were not significant (Fig. 7). During the three measurement days, mean values for soil evaporation were 0.15–0.28 mm d^{-1} and for evapotranspiration they were 0.7–0.9 mm d^{-1}.

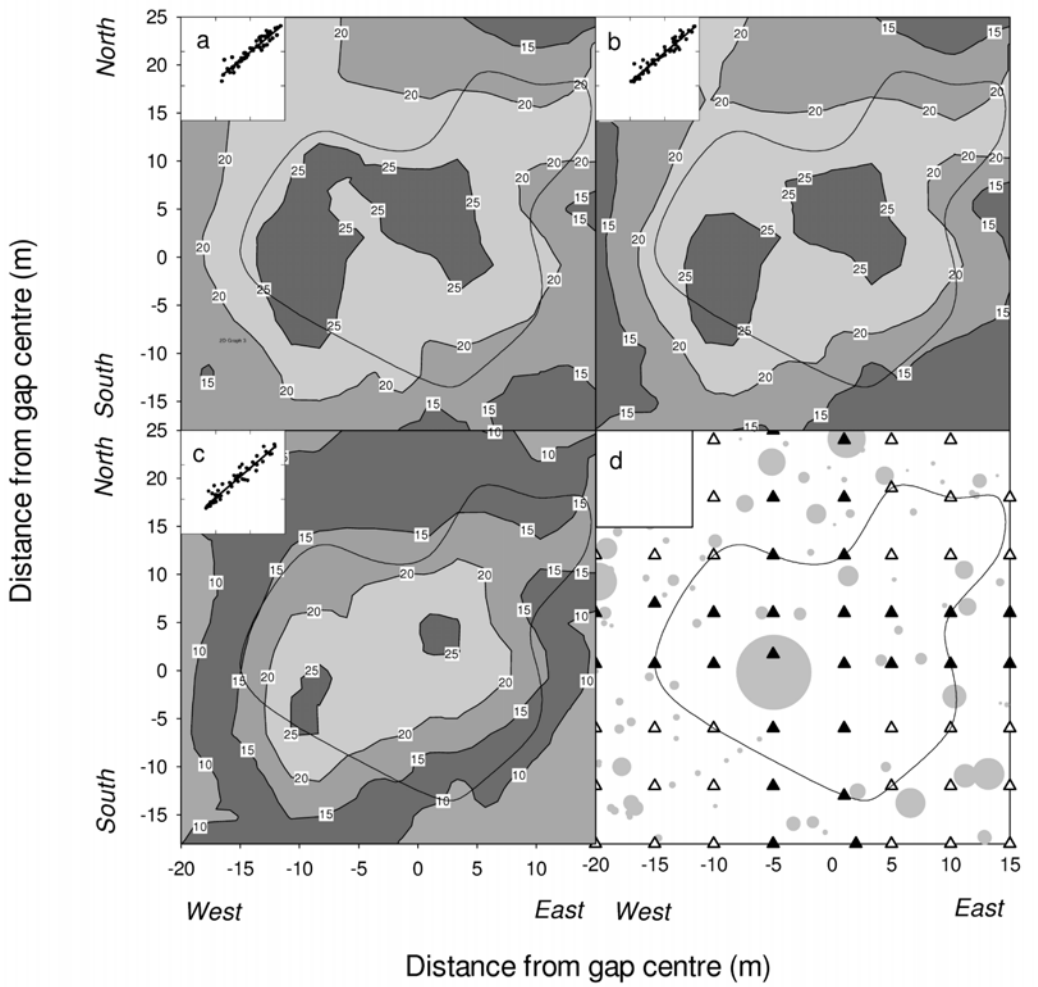

Fig. 5. Smoothed values of soil water content at 0–0.5 m depth (SWC_{50}, vol.%) in and around a canopy gap in Suserup Skov during the summer of 2000. Inserts show measured vs predicted (smoothed) values with all axes from 0 to 30 vol.%; r^2 values are given subsequently. (a): mean for July (n = 7; $r^2 = 0.91$), (b): mean for August (n = 9; $r^2 = 0.93$), (c): lowest observation on 1 September (r^2=0.92), (d): location of trees in and around the gap (gray circles). The size of the circles is scaled from tree diameter. The gap centre is at (0.0) m. At (–5.0) m a large grey circle show the position of the gap maker, which is still alive albeit with a very small crown. A thin black line indicates the edge of the gap. Triangles show positions where throughfall and soil moisture was measured until April 2001. Black triangles are positions measured after April 2001. For the contour plots, data are smoothed using a negative exponential weighting procedure (SigmaPlot 2000, SPSS, USA) with fixed bandwidth and a sampling proportion of 0.2 (ca 5 observations for each prediction; modified from Ritter et al. 2005).

Tree transpiration – effects of size and position of trees

For the three groups of trees the weekly value of mean daily transpiration were 0.2–0.9 mm (sub_F), 0.3–0.8 mm (sub_O) and 0.4–1.3 mm (can). The minimum values were reached in mid September except for sub_O where minimum was reached in late June. Maximum values were reached in mid June for all groups. Monthly values of J_{s-sum} and J_{s-max} were higher for sub_O than for sub_F in August ($(p<0.1)$ J_{s-sum}: 1022 and 689 kg m^{-2} d^{-1}; J_{s-max}: 77 and 50 kg m^{-2} $halfhour^{-1}$ respectively) and September 2000 ($(p<0.05)$ J_{s-sum}: 749 and 410 kg m^{-2} d^{-1}; J_{s-max}: 65 and 34 kg m^{-2} $halfhour^{-1}$ respectively), thus not in early summer. For E_{sum} in weekly resolution

Table 3. Mean soil water content in the intact forest, edge and canopy gap for Suserup Skov, Denmark June 2000–October 2001. Different letters indicate significant differences among categories ($p<0.05$) using a Tukey-Kramer adjustment for multible comparisons. From June 2000 to April 2001 differences are tested for: 1) the 59 positions in the grid; 2) the 28 positions measured throughout the period. Results from 2) are given in brackets.

Soil water content (vol.%)	0–0.9 m Forest	Gap	Edge	0–0.3 m Forest	Gap	Edge
June–September 2000	^{A}15.6 (^{a}15.1)	^{B}23.5 (^{b}24.1)	^{C}19.4 (^{c}19.2)	^{A}17.7[1] (^{a}17.5)	^{B}27.6[1] (^{b}28.6)	^{C}22.8[1] (^{c}24.1)
October–December 2000	^{A}16.9 (^{a}16.5)	^{B}24.6 (^{b}25.3)	^{C}20.8 (^{c}20.8)	^{A}22.4 (^{a}22.0)	^{B}30.0 (^{b}30.9)	^{B}27.2 (^{b}27.8)
January–19 April 2001	24.7 (^{a}24.5)	26.1 (^{b}26.2)	25.9 (^{b}26.0)	^{A}28.7 (^{a}28.0)	^{AB}30.6 (^{b}31.2)	^{B}31.0 (^{b}31.4)
20 April–May 2001	^{A}22.2	^{B}24.6	^{AB}23.7	^{A}23.6[1]	^{B}28.0[1]	^{AB}26.6[1]
June–September 2001	^{A}16.7	^{B}24.3	^{A}19.9	^{A}19.9	^{B}29.2	^{C}24.5
October 2001	^{A}20.9[1]	^{B}26.8[1]	^{B}25.2[1]	^{A}25.8[1]	^{B}32.5[1]	^{AB}29.5[1]
Fraction of field capacity	0–0.9 m			0–0.3 m		
June–September 2000	^{A}0.64 (^{a}0.61)	^{B}0.90 (^{b}0.92)	^{C}0.75 (^{a}0.73)	^{A}0.63 (^{a}0.63)	^{B}0.90 (^{b}0.91)	^{C}0.75 (^{c}0.77)
October–December 2000	^{A}0.70 (^{a}0.67)	^{B}0.94 (^{b}0.96)	^{C}0.79 (^{c}0.79)	^{A}0.78 (^{a}0.78[1])	^{B}0.98 (^{b}0.98[1])	^{C}0.88 (^{c}0.89[1])
January–19 April 2001	1.00 (1.00)	1.00 (1.00)	1.00 (1.00)	^{A}1.00 (1.00)	^{A}1.00 (1.00)	^{A}1.00 (1.00)
20 April–May 2001	^{A}0.91	^{B}0.94	^{AB}0.91	^{A}0.83	^{A}0.89	^{A}0.84
June–September 2001	^{A}0.68	^{B}0.93	^{A}0.76	^{A}0.71	^{B}0.93	^{A}0.78
October 2001	^{A}0.89[1]	^{B}1.02[1]	^{A}0.95[1]	^{A}0.89	^{B}1.03	^{A}0.94

[1] The response variable was transformed. The mean value was back-transformed.

significant differences were predominantly found between can and sub_F and values were consistently highest for the former (Table 4 and Fig. 8). Significant differences were found beginning in mid July 2000 until the end of the measurement period, thus not in the early summer. The evolution of the mean daily J_{s-sum} (weekly resolution, Fig. 8) shows that in early summer subcanopy trees are equal regardless of position and canopy trees show the highest values. In late summer subcanopy trees near the gap show the highest values, canopy trees intermediate values and subcanopy trees below the forest canopy show the lowest values. This development is seen also for E_{sum} (Fig. 8, lower panel). In the multiple linear regression analysis on the relative daily flux density for both can and sub_F, global radiation ($p<0.0012$; $p<0.0001$) and available soil water ($p<0.0001$; $p<0.001$) both influenced the relative difference in sap flux density of can/sub_O and sub_F/sub_O (see also inserts in Fig. 8). The diurnal variation in J_s for the three groups during three selected days in 2000 is seen in Fig. 9. In June all three groups showed similar diurnal curves for J_s. In July the groups show similar values, but there is a tendency that subcanopy trees below the canopy

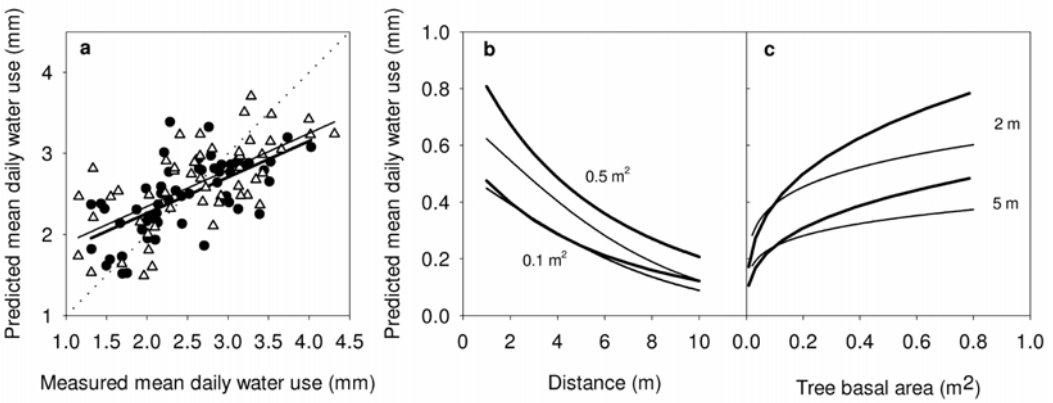

Fig. 6. Results from the prediction of water use in Suserup Skov. (a): Predicted and observed water use in 0–0.5 m depth (19 d, black symbols, thick line) and in 0–0.9 m depth (14 d, open symbols, thin line). For both depths r^2=0.43. Parameter values were: a = –6.0947, b = –2.3048, c = 0.1135, d = 0.3290 (0–0.5 m) and a = 2.2437, b = 0.7895, c = 0.2453, d = 0.2946 (0–0.9 m). The dotted line show a 1:1 relationship, (b): predicted water use vs distance and two examples of tree basal area, (c): predicted water use vs tree basal area with two examples of distance.

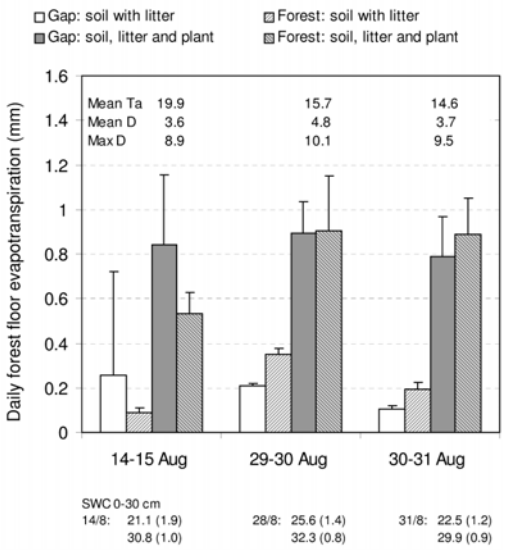

Fig. 7. Evapotranspiration from the forest floor in gap and forest positions August 2001 in Suserup Skov. For 29–30 and 30–31 August observations were made on the same lysimeter and soil volume. Error bars show 1 standard error of the mean (n=4). The daily mean air temperature (Ta, °C) and the daily mean (D) and maximum (max D) vapour pressure deficit (hPa) are shown above bars. Soil water content (vol.%) in 0–0.3 m depth was measured on 14, 28 and 31 August. These data are shown below bars (upper: forest; lower: gap) including the standard error of the mean in parenthesis.

are lower than the remaining groups. In August there seems to be a clear differentiation among groups (sub_O > can > sub_F).

Discussion

Spatial patterns

Throughfall was higher in the gap than in the intact forest positions both annually and for spring and summer periods. In the growing season Slavík et al. (1957, in Geiger et al. 1995) found 90–100% of reference precipitation in the gap and 70% in the intact forest, which corresponds well to that found in Suserup Skov. Neal et al. (1993) found significantly increasing throughfall in plots after windthrow (storm damage) but the size of the openings created were not given. Zirlewagen and von Wilpert (2001) found annual interception loss in gaps and crown openings to be 21% of reference precipitation, which is higher than in Suserup Skov (15%). In the study mentioned above the height of the water collectors relative to the possible ground vegetation is not given thus a direct comparison may be misleading. Assuming that they measured above the ground vegetation and at a similar height as in Suserup Skov the difference still does not seem unreasonable as some of these gaps were small corresponding to only one tree crown in size. When gaps are formed branches and leaves in the canopy are removed and throughfall should logically increase, however, the creation of canopy openings also increases turbulence and hence interception losses (Neal et al. 1993). The resulting increase in throughfall thus depends on gap size (rain shadow from stand, Geiger et al. 1995) and turbulence as well as rainfall duration and -intensity (Rutter 1975). The interception loss in winter did not differ among positions. Except from the lack of leaves at positions in the intact forest, this is presumably caused by high turbulence increasing interception losses in gap positions. Further, rainfall patterns differed between summer and winter: high intensity rain storms occurred mostly in summer with peak intensities of 15–27 mm d^{-1} in 2000 and 15–38 mm d^{-1} in 2001, whereas peak values for winter observations were below 15 mm d^{-1}.

Stemflow in the intact forest when bare was estimated at 6.0% of precipitation and 2.2% when in leaf. This corresponds to measurements in European beech (Neal et al. 1993), but the values are lower than found by Granier et al. (2000a) in the growing season and in studies reviewed by Ladekarl (2001) for pure stands of European beech. Common ash has a more coarse textured bark than European beech and stemflow is therefore expected to be lower for

Table 4. Comparison (t-test) of mean daily E_{sum} (weekly mean) for tree groups in Suserup Skov, Denmark 15 June–30 September 2000. P-values are indicated as p<0.1 (*) and p<0.05 (**).

Week number	Comparison sub_O/can	sub_F/can
E_{sum} (mm d^{-1})		
1: Mid June	0.75/1.22**	ns
2: Mid June	0.76/1.25**	0.87/1.25*
3: Late June	ns	ns
4: Early July	ns	0.69/1.08*
5: Mid July	0.55/0.87*	0.50/0.87**
6: Mid July	ns	0.48/0.76*
7: Late July	ns	0.45/0.76*
8: July/August	0.50/0.73*	0.36/0.73**
9: Early August	ns	0.50/0.88*
10: Mid August	ns	0.51/0.87*
11: Late August	ns	0.53/0.94*
12: August/September	ns	0.35/0.63*
13: Early September	ns	0.28/0.54**
14: Mid September	(–)	(–)
15: Mid September	(–)	(–)
16: Late September	ns	0.25/0.55**[1]

(–) Due to non-homogeneity of variance results were not interpreted.
[1] The response variable was log-transformed.

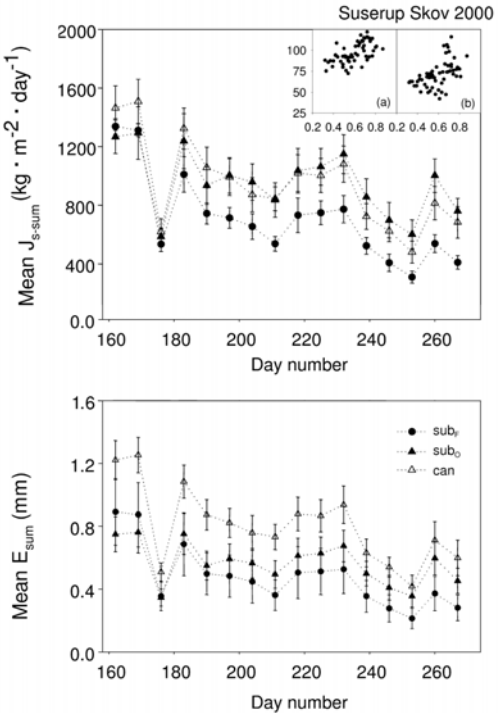

Fig. 8. Weekly values of the mean daily tree sap flux density (upper) and daily tree transpiration (lower) in European beech *Fagus sylvatica* in Suserup Skov in the summer 2000. E_{sum} is the transpiration for unit projected crown area. Error bars show ± one standard error of the mean. Inserts in the upper panel show daily sap flux density (as % of sub_O) vs available soil water below the intact forest (a) for can and (b) for sub_F; see text (Dalsgaard unpubl.).

the mixed stand than for a pure stand of European beech. For the same BA common ash had approximately half the stemflow of European beech. Differences in crown geometry between the two species as well as bark texture could contribute to the observed differences. Further, in a natural stand individual trees could be expected to have lower stemflow than in managed stands due to irregular stem shapes and the coarser texture of old and damaged trees (Levia and Frost 2003).

Net-precipitation (throughfall 80% of P + stemflow 6% of P) during the winter was higher in the intact forest than the observed throughfall in the gap positions (78% of P). For gap positions without ground vegetation the net-precipitation equals throughfall, but for positions with dense ground vegetation (regenerating plants) net-precipitation was not determined. In edge positions stemflow may have been higher than in the intact forest thus also net-precipitation (throughfall 82% of P + stemflow 12% of P).

In Suserup Skov, throughfall in autumn was higher in the northern part of the measurement area presumably because of wind (from the lake, south of the measurement plot), however, this was not tested. Slavík et al. (1957, in Geiger et al. 1995) found a similar effect at the eastern edge of a gap.

SWC as well as RSWC were significantly higher in the gap than in intact forest positions throughout most of the year for both the upper soil layer (0–0.3 m) and for the soil down to a depth of 0.9 m expected to cover most of the rooting zone. During the winter there was no effect of the gap on RSWC and only small differences among categories for SWC. For most of the periods SWC in the southern and southeastern parts of the gap were significantly lower than remaining parts of the gap. As there was no differences in elevation among positions this indicated that soil texture may vary across the measurement area. During site installation a high stone content was observed in the southern part of the gap (unpubl., Rajzek pers. comm.). Comparisons among categories are probably best when based on the RSWC values. High throughfall at the northern gap edge (possibly caused by wind from the southern direction) as well as high stemflow on edge trees probably also contributed to these differences. Though this study showed large differences in stemflow for the two species and for trees of differing exposure, the resolution for soil moisture measurement (monthly to bi-weekly measurements in an approximately 5 × 5 m grid) does not allow for a detailed study of the influence of stemflow on soil moisture.

Higher soil moisture in the gap than in intact forest positions have been found in numerous studies (Bauhus and Bartsch 1995, Ostertag 1998, Heinemann et al. 2000, Gray et al. 2002). The ratio of gap diameter to stand height in Suserup Skov is ca 0.6. Gray et al. (2002) observed that gaps with ratios of 0.4–0.6 showed the highest response in soil moisture to gap formation compared to both smaller and larger gaps.

Water use in 0–0.5 m depth was correlated with tree diameter and distance in spite of the high spatial heterogeneity in both soil and vegetation. The solution of Eq. 1 resulted in a model for water use that resembled that for fine root biomass (Nielsen and Mackenthun 1991); decreasing predicted water use with increasing distance. Ammer and Wagner (2005) used models with decreasing fine root biomass with distance (maximum reached at some distance from the stem) and Wang et al. (2002) found that fine roots were relatively evenly distributed and their densities not related to the distance to trees. Thus, the assumptions in the model used in the present study may not be optimal, but rather show a starting point based on the distribution of fine roots in European beech (Nielsen and Mackenthun 1991). The fact that the predicted water use does not lay near the 1:1 line in Fig. 6a signalizes that the assumptions of the model are not fully valid. The site in Suserup Skov is complex in structure, which is probably the reason for the rather low r^2 value. Trees have not been spaced evenly by forest management (thinning), thus the

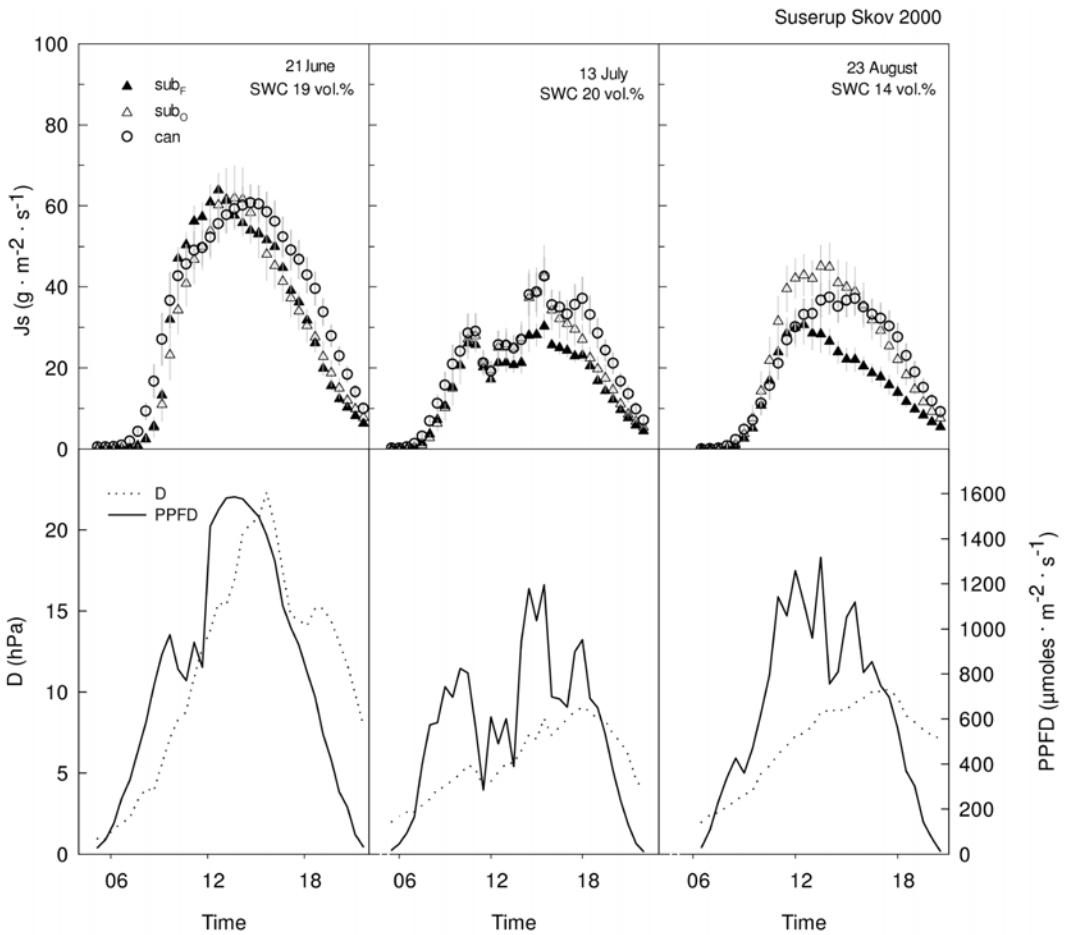

Fig. 9. Diurnal variation of sap flux density (J_s, upper panel) for European beech *Fagus sylvatica* for three groups of trees in Suserup Skov in the summer 2000. Errors bars show ± one standard error of the mean. Soil water content (SWC) is indicated on the graphs and represents a 0–0.5 m soil profile below the forest canopy (n=10). Air vapor pressure deficit (D) and photosynthetic global radiation (PPFD) are shown in the lower panel (Dalsgaard unpubl.).

roots may not be distributed symmetrically around the tree stems as assumed in the model. Roots of different species occupy different patches in the soil and European beech fine roots have been found to colonize nutrient rich patches more successfully than sessile oak *Quercus petrea* (Leuschner et al. 2001). In the unmanaged Suserup Skov decaying logs could contribute to spatial heterogeneity in soil nutrients. Common ash showed a plate root system and European beech a deeper growing heart root system (Rust and Savill 2000). In a mixed stand with European beech and Norway spruce European beech coarse roots primarily occupied the deep soil layers and Norway spruce primarily the upper soil layers (Schmid and Kazda 2001). To better predict the spatial variation of water use in mixed, uneven-aged stands it is relevant to incorporate the effects of spatial variability in soil nutrients as well as species-specific rooting patterns. The 19 d used for WU_{50} and 14 d for WU_{90} were presumably characterized by vigorous root growth. The positions with the highest water use could have changed with time, this not being reflected in input variables. It was expected that when using $WU_{90,}$ the regression of the predicted vs the observed water use would be closer to the 1:1 line than for WU_{50}, especially for positions with high BA and high water use. However, this was not found. Evapotranspiration from soil and ground vegetation was not included in the model, but these were up to 0.9 mm d^{-1} (up to 0.3 mm d^{-1} for soil; present study, measurements in 2001). Thus, they clearly contributed to the measured water use. Though ground vegetation probably contributed less to water use in 2000 than in 2001 (plants were smaller)

the inclusion of this process is likely to improve the predictions of spatial variability of water use in the gap. In gap positions soil water content was near field capacity in the summer months, thus seepage of water beyond 0.5 cm soil depth could also have contributed to the relatively poor model fit. Seepage during the summer can, however, be assumed to be very low at this site as it is not a sandy soil. The small rain episodes during the sample periods (< 1 mm) were all lower than the water holding capacity of the canopy and of the litter layer of a temperate deciduous forest (2 mm, Wilson et al. 2000) and should not have affected the results. It is concluded that the model is still too coarse to predict the extent of root gaps. The species distribution near specific measurement positions influenced the residuals of the model thus with improvements it may be possible to detect significant species effects of rooting patterns and water use in mixed stands.

In the small gap in Suserup Skov forest floor evapotranspiration did not differ between gap and intact forest positions. This is surprising knowing that more light penetrates to the floor in a gap than below the forest canopy (Ritter et al. 2005). However, the lysimeter measurements represent only a few days and these were not hot summer days. Also, this late in summer (mid–late August), the amount of direct radiation reaching the forest floor may be low. The small lysimeters, chosen for the ease of installation, may not have enclosed all roots in the cases where plants were included. Evaporation may thus be underestimated. However, it is likely that uptake by roots within the lysimeter soil volume were able to meet the evaporative demand and thus compensated. For technical reasons it was unfortunately not possible to compare lysimeter measurements with changes in SWC measured by TDR. The forest floor evaporation has been shown to be driven mainly by large scale eddies penetrating the forest canopy thus being closely coupled to the vapor pressure in the ambient air (Baldocchi and Meyers 1991). This would explain the lack of differences between the intact forest and gap positions. More measurements of soil evaporation and forest floor evapotranspiration could be valuable to further test this hypothesis.

Fluxes

Drainage of water beyond the rooting zone can be expected to be higher in gap than in the intact forest positions because of a lower canopy interception and a lower transpiration. Higher drainage in gap positions was found by Zirlewagen and von Wilpert (2001) and by Vilhar et al. (2005), though in the latter study (growing season only) this difference was not pronounced. Rather, it was concluded that, in a natural forest with a heterogeneous stand and soil structure, drainage fluxes were not closely related to the position relative to the gap centre. A higher input from stemflow in the intact forest (and edge) than in the gap may counterbalance the differences caused by throughfall and transpiration. Model examination of drainage fluxes in Suserup Skov is not completed. However, based on measurements the following can be expected: Soil moisture in gap positions remained near field capacity in summer. This indicates that drainage in autumn/winter will start earlier in gap than in intact forest positions where field capacity is reached as late as December or January at some positions. For the 2000 growing season it was estimated (Ritter et al. 2005), that lower transpiration in the gap was the major cause for the differences in soil moisture among gap and intact forest positions. The estimated amount of precipitation from mid June to September was 45 mm (the equivalent of 5 vol.% in a 0.9 m deep soil profile), whereas transpiration in the closed stand was ca 144 mm in the same period (Dalsgaard et al. unpubl.), a flux assumed to be almost lacking in the centre of the gap. A conservative estimate of forest floor evaporation of 0.2 mm d^{-1} adds up to 13% of stand evaporation in dry conditions in the same period. This is higher than closed European beech forest (Granier et al. 2000a), but other studies in natural temperate deciduous forests have found that evaporation from the forest floor was 10–20%, thus a relatively large part of total evapotranspiration (Kelliher et al. 1992). The water-holding capacity of the litter layer was found to control the amount of forest floor evaporation (Wilson et al. 2000).

Effects and temporal trends

In Suserup Skov, a higher transpiration for canopy than for subcanopy trees was found as also in other studies (Ladefoged 1963, Strelcová et al. 2002, Köstner et al. 1992), however, the differences among trees in different canopy position varied according to the amount of available soil water. Subcanopy trees near the gap benefited from the high soil moisture and maintained high transpiration throughout the summer. European beech has been reported both to be a drought sensitive species (Backes and Leuschner 2000, Aranda et al. 2000) and to exhibit a response in canopy conductance to low soil moisture similar to more drought tolerating species (Granier et al. 2000a, b). Unfortunately it was not possible to investigate transpiration for different species in the present study. When available soil water in the intact forest approaches 40% of the potential it can be expected that tree transpiration is reduced (Granier et al. 2000a, b), whereas trees near the gap will maintain a higher rate of transpiration due to a higher soil moisture. In periods of water stress growth of suppressed trees are affected more negatively than dominant or open grown trees (Piutti and Cescatti 1997, Cescatti and Piutti 1998). In the beginning of the measurement period (mid June 2000) subcanopy trees below the canopy had higher or similar rates of sap flux density and transpiration than those near the gap. This was contrary to expectations because transpiration from trees at the edge of the

gap was expected to be higher also early in the growing season because of more light reaching the crowns. Trees are able to displace their crowns toward gap centres and thereby forage for light (Muth and Bazzaz 2002). Based on results from Suserup Skov it is suggested that not only light determines the growth of trees in the edge of a canopy gap, but that the higher soil moisture availability in gaps significantly contributes to tree growth. Thus, that the spatial (and temporal) variation in available soil moisture has implications for forest succession and structure. Catovsky et al. (2002) found in closed forest stands that sap flow was a good measure of whole tree function across tree species including the overall carbon gain and stem growth. Soil nutrients have been found to be more abundant in gaps than in the adjacent intact forest (Ritter and Vesterdal 2006). In addition to higher soil moisture this may also improve the growing conditions of trees in the edge of canopy gaps.

For how long do the effects of a canopy gap persist? Results from the analyses of relative soil water content (RSWC) showed that edge was a distinct category in 2000 only and in 2001 mostly was not to be distinguished from the intact forest category. Throughfall in the gap during summer was higher in 2000 than in 2001. Further, soil water content (0–0.3 m) along a transect from south to north through the gap showed that soil water content decreased from 2000 to 2001 in the northern, but not in the southern part (Ritter et al. 2005). It was observed in the field that regeneration grew rapidly especially in the northern part of the gap and tree density was higher in the northern than in the southern gap edge. Taken together this is an indication that only one year after gap formation edge trees and regenerating plants had already started to influence the gap area by root and crown growth and thereby water extraction from the soil as well as rain interception.

Valverde and Silvertown (1997) found that gap closure rates are highest immediately after gap formation and that gap closure (based on hemispherical photography) is completed after ca 9 yr in temperate forests. Unfortunately the study in Suserup Skov does not allow the estimation of the time used for gap closure of either above or below ground gaps. However, the measured water use for each position for 19 d (WU_{90}) in the summer 2000 had a minimum value of 24.9 mm. That is > 1 mm d^{-1}. This is more than what could be expected from bare soil evaporation, thus roots must be active even in the central parts of the gap. Other studies have found that below ground gaps disappear quickly (1 and 4 yr after gap formation) (Veenendaal et al. 1995, Gray et al. 2002). Observations in Suserup Skov tend to support this result.

Conclusions

In a small canopy gap (diameter < stand height) in Suserup Skov during the first and second growing season soil water content in both 0–0.3 and 0–0.9 m depth was significantly higher in gap positions than in the intact forest in spring, summer and autumn (hypothesis 1). For the relative soil water content differences were clear in summer and autumn. Soil moisture was near 90% of field capacity in the gap during the summer months compared to 60–70% in the intact forest. There was no evidence that positions north of the gap centre were drier than remaining plots due to more incoming radiation. For the relative soil water content, edge was a distinct category in summer and autumn 2000, but not in 2001 where edge was equal to the intact forest category. Annual throughfall (hypothesis 2) was 17% higher in the gap than in the intact forest (85 and 73% of P respectively). Throughfall was higher in the gap than in the intact forest in spring and summer, but not in autumn and winter. In the autumn precipitation was significantly higher north of the gap centre than in other positions. Throughfall in the gap was higher in the first than in the second summer after gap formation. Stemflow (hypothesis 3) was higher for European beech than for common ash (ca 2:1 for unit basal area). For both species stemflow was higher when bare than when in leaf (2:1 for unit basal area) and exposed trees (when bare) showed the highest stemflow volumes. On a stand level stemflow was 2% of P in summer, 6% in winter and 12% in winter for exposed trees. Water use (hypothesis 4) during 19 d (0–0.5 m depth) or 14 d (0–0.9 m depth) was correlated (r^2 = 0.43) to tree basal area and distance using a non-linear model previously used to predict spatial variability in root biomass. It was not possible to parameterize species specific models. But there was a tendency for residuals to depend on the species dominance at the measurement positions. Forest floor evapotranspiration (hypothesis 5) did not differ between gap and intact forest positions. This was contrary to the expectation. Individual tree transpiration (hypothesis 6) showed that high soil moisture in the gap enabled released subcanopy trees of European beech to sustain high transpiration rates throughout the growing season (2000), whereas transpiration rates of canopy and suppressed subcanopy trees of European beech were limited by low soil moisture.

The formation of a canopy gap clearly affected the hydrological cycle but it is suggested that these changes are very short lived. Soil moisture in edge positions approached that of the intact forest in the second growing season and throughfall in the gap decreased (relative to P). The sustained transpiration in edge trees during the summer also indicate that these trees may grow vigorously.

Thus, processes influencing soil moisture can affect gap dynamics through the facilitation of gap closure. The effect of gap formation on seepage water (if any) should be quantified using a suitable process based model.

Working in a semi-natural forest like Suserup Skov presents obvious technical and methodological problems. Variability in investigated objects (soil, trees and classes of canopy cover) is large because each measurement position

and each tree has its own history of disturbance, damage and competition. This variability obscures the mean values, but must also be regarded as an important part of the results. Results reported here are from the two first growing seasons after formation of one small canopy gap. More gaps should be investigated to test the generality of these results. To increase our knowledge on the interaction between above and below ground processes monitoring should best continue until both above and below ground gaps are closed.

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Paper III

Beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) sap flow in a natural deciduous forest in Denmark – interactions between forest dynamics and soil water variability near a canopy gap

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Running head: Tree sap flow near a canopy gap

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Summary

The objective of this study was to investigate the seasonal course of sap flow (J_s, g $m^{-2}s^{-1}$) for beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) during a progressive soil drought near a recently formed canopy gap where soil moisture remained high throughout the vegetation period. For beech, transpiration (E) was calculated from crown projection area and the radial variation in J_s (0-60 mm) found from on-site measurements. It was hypothesized that i) seasonal soil drought limits J_s (integrated daily to $J_{s\text{-}sum}$) for trees in the closed forest but not those at the gap edge and ii) trees beneath the closed forest canopy experience a more severe limitation in $J_{s\text{-}sum}$ than canopy trees. Regression analyses showed that $J_{s\text{-}sum}$ was significantly reduced (by 29-39%) for canopy trees and for subcanopy trees in the closed forest with the progression of soil drought, but not for released trees at the gap edge. Mean $J_{s\text{-}sum}$ for trees at the gap edge was significantly higher than for trees in or beneath the closed canopy in August and September, but not in early summer. Trees beneath the closed canopy and canopy trees showed similar mean $J_{s\text{-}sum}$ during the summer, but trees beneath the canopy experienced a slightly higher limitation in E. J_s declined with increasing xylem depth. The relatively moderate decline may be specific to this site and related to tree structure e.g. rooting depth. J_s in ash was lower than in beech and possibly influenced by inactive xylem. It is concluded that the high availability of water in gaps mitigates the effects of drought for trees near the gap. It is suggested that this benefits the growth for trees near the gap and influences the rate of gap closure.

Keywords: Mixed forest, sap flux density, stratified canopy, tree water use.

Introduction

In natural forests dominated by beech (*Fagus sylvatica* L.) the decay and fall of canopy trees creates gaps where above and below ground resources are made available to seedlings and saplings (Koop and Hilgen 1987, Emborg et al. 2000). Mature trees at the edge of a canopy gap react to gap formation by lateral growth of the tree crown (Hibbs 1982) and by displacement of tree crowns toward areas with high light availability (Muth and Bazzaz 2002). However, the resources released below ground may also affect the edge trees. Müller and Wagner (2003) observed that roots of edge trees grew toward the gap area and Cienciala et al. (2002) found that water use was higher for trees at a northern forest edge than for trees in the forest interior. In and near a canopy gap, soil water displays a high spatial and temporal variability. With the progression of soil drought during the growing season the soil water content decreases below the closed forest canopy but remains high and relatively stable in the centre of recently formed gaps (Gray et al. 2002, Ritter et al. 2005). Trees growing at the edge of a gap with access to ample soil water may not experience any drought. This is in contrast to trees in the closed forest where competition for soil water frequently limits transpiration (Granier et al. 2000a, b). Limitation of transpiration due to seasonal drought may be more severe for suppressed than for dominant trees (Piutti and Cescatti 1997) possibly due to differences in rooting depth (Dawson 1996). Thus, the spatial and temporal distribution of soil water may affect tree growth and forest development. Sap flow in trees has been found to be a good indicator for growth and vitality (Catovsky et al. 2002, Vincke et al. 2005). Sap flow of individual trees could provide insight into the importance of soil water variability for the forest dynamics and structure following small scale disturbances. The main objective of the study was to describe the seasonal development in sap flow and transpiration for trees according to their size, species and position relative to the gap. A second objective was to develop a simple model of the radial variation in sap flow in beech used to calculate tree transpiration. It was hypothesized that i) seasonal soil drought limits sap flow for trees in the closed forest but not those at the gap edge and ii) trees below the main canopy experience a more severe limitation in sap flow than canopy trees. The interaction between forest dynamics and soil water variability in an unmanaged natural forest is viewed as a useful and important point of reference for forest research and management (Hahn et al. 2007). Knowledge on the functionality of natural forests and the response to canopy gaps

is particularly relevant for forest management applying single tree or group selection systems.

Methods

Study site

The study was conducted in Suserup Forest, a 19.2 ha mixed deciduous forest reserve in eastern Denmark (55°22´N, 11°34´E). It borders a lake to the southwest and is otherwise surrounded by fields. The mean annual precipitation 1961-1990 is 644 mm with the majority falling in late summer and fall (Frich et al. 1997). The mean annual air temperature 1987-1997 is 8.1 °C (Laursen et al. 1999). Parameters describing the stand structure are listed in Table 1. Measurements for trees > 45 mm stem diameter included height (to highest point of crown), position and stem diameter at 1.3 m height as well as the height of the crown base and crown radii in eight directions. Measurements were conducted in a 6400 m^2 area in January 2000 and in the following winter. Beech trees were recorded up to a stem diameter of 1.4 m. The oldest beech trees were approximately 300 years of age (Emborg et al. 2000). The soil is a loamy till with pockets of sandy till developed from moraine deposits and classified as an Inceptisol (Vejre and Emborg 1996, Ritter and Vesterdal 2006). In-situ field capacity in 0-0.9 m depth obtained as the mean of monthly soil water content measurements January to April was 25.4 vol.%, the equivalent of 228 mm. The measurement site was on a well-drained plateau in the central part of the forest approximately 80 m from the northern forest edge. It includes a small and irregularly shaped gap of approximately 20 m diameter formed after a hurricane in December 1999. The forest was protected from live-stock in 1807. Thereafter silvicultural management was limited (Fritzbøger and Emborg 1996, Hannon et al. 2000, Heilmann-Clausen et al. 2007).

Meteorological and soil water content measurements

Two weather stations were placed at the site, one in the forest below the closed canopy, near the trees sampled for sap flow measurements, and one in an open field approximately 300 m from the northern forest edge. At both stations measurements were taken in 2 m height every 10 s. Measured variables were relative air humidity (RH, %), air temperature (T_a, °C) (HMP45C used with

standard shielding, Vaisala, Helsinki, SF) and wind speed (u, m s^{-1}) (A100L2 cup anemometer, Vector Instruments, Denbighshire, UK). In addition the open-field station measured the photosynthetically active radiation (PPF, µmol m^{-2} s^{-1}, LI190SA Quantum Sensor, Li-Cor, Lincoln, NE, USA) and precipitation (P, mm, Rain-o-matic, Pronamic, Silkeborg, DK). 10 min averages were stored in the forest station to a DL2e (Delta-T Devices Ltd, Cambridge, UK) and in the open-field station to a DT50 (dataTaker Pty Ltd., Rowville, AU). 30 min averages were calculated from these measurements. The daily global radiation (R_g, J m^{-2} day^{-1}) was calculated from PPF (Monteith and Unsworth 1990, Lambers et al. 1998). The air vapor pressure deficit (D, hPa) was calculated from measurements of RH and T_a (Buck 1981). Manual measurements of the volumetric soil water content (SWC, vol.%, Tektronix 1502C/1502B, Tektronix inc., Berkshire, UK) were obtained biweekly using Time Domain Reflectometry (Topp et al. 1980). The stationary probes consisted of two 0.5 m long stainless steel rods with a diameter of 6 mm and a distance of 50 mm. Probes were installed vertically from the undisturbed soil surface in a grid with 59 positions (Figure 1). Measurements were in the gap (open conditions, n=13), the closed canopy (behind the first row of trees bordering the gap, n=29) and the gap edge (n=17).

Sap flow

Two time series of sap flow (J_s) are presented in this study 1) data from 12 beech and six ash (*Fraximus excelsior* L.) June 15 - September 30, 2000 for the evaluation of J_s during the growing season in trees of different sizes and social positions, and 2) data from four of these trees July 5 – 12, 2001 for the evaluation of the radial variation in J_s in the diffuse porous beech. J_s (g m^{-2} s^{-1}) was measured using the thermal dissipation method (Granier 1985, 1987). For each measurement position, two 20 mm long and 2 mm diameter probes (ProBit, Freiburg, Germany) were inserted radially into the stem below bark 2 m above the ground with a vertical distance of 0.20 m. The upper probe was heated by a constant current adjusted in the field to 120 mA (± 1 mA). Heat conducting paste was applied to the probes before installation (the upper heated sensor in an aluminum pipe). The installation was protected from water intrusion by silicon paste and covered by protecting cups, insulating foam and blankets with a reflective surface to protect from heating by direct sunlight. Measurements in mV were made for every 60 s and 30 min averages were stored (DL2e, Delta-T Devices Ltd, Cambridge, UK). In June 2000, one set of probes were inserted into the northern side of the stem for

each of 18 trees positioned north west of the gap (Figure 1 and Table 2), measuring J_s in the outer 20 mm of the xylem. In July 2001, each of the four selected beech canopy trees (Table 2) was equipped with three sets of probes measuring J_s in 0-20, 20-40 and 40-60 mm xylem depth. The horizontal distance between each set of these probes was 0.20 m.

Data processing and statistical analyses

Radial variation in sap flow

In 2001 measurements of sap flow in three xylem depths were denoted $J_{s0\text{-}20}$ (0-20 mm), $J_{s20\text{-}40}$ (20-40 mm) and $J_{s40\text{-}60}$ (40-60 mm). For the formulation of a model used to scale measurements in the outer xylem (0-20 mm) to the whole tree, J_s was integrated for the measurement period of eight days in July, 2001, and a mean for each measurement depth of the four trees was calculated as presented in Köstner et al. (1998). These means were normalized relative to $J_{s0\text{-}20}$. A logistic model was chosen and it was assumed for the formulation of the model that environmental variables were constant. The model supports the assumption that J_s decreases with depth and approaches zero (Lüttschwager and Remus, 2007), but remains positive.

Eq. (1)
$$y = \frac{a}{1 + \left(\frac{x}{x_0}\right)^b}$$

y is the relative J_s, x is the depth (cm) of the mid point of the sensor and a, b and x_0 are fitted parameters, where a is the maximum, b is a shape parameter and x_0 places the curve on the x-axis.

Temporal variation in sap flow and the relationship to D, R_g and SWC

In 2000, J_s (0-20 mm xylem depth) was summarized as the daily sum ($J_{s\text{-}sum}$, kg m^{-2} day^{-1}), the daily maximum ($J_{s\text{-}max}$, g m^{-2} s^{-1}), the daily transpiration (E_{sum}, mm) and the daily maximum transpiration (E_{max}, mm 30 min^{-1}). For ash only J_s, $J_{s\text{-}sum}$ and $J_{s\text{-}max}$ are presented and results were not included in all the statistical analyses.

The depth of the sapwood in ash was not measured and presumably the 20 mm long probes extended beyond the sapwood which has been measured by Cochard et al. (1997) to approximately 10 mm. Scaling of J_s to tree transpiration (E) in beech used Eq. (1) fitted to the measurements in 2001 to integrate J_s over the stem cross sectional area to a lower threshold of a predicted relative J_s of 0.05. This value of relative J_s occurs at approximately 130 mm xylem depth. To estimate E the calculated amount of water transported in the stem was related to the crown projection area found from measurements of crown radius in 8 directions assuming eight triangular sections.

For the statistical analyses, trees were classified according to their height and position relative to the canopy gap. Trees 14-20 m tall were subcanopy trees (SUB) and trees 25-34 m were canopy trees (CAN). Trees at the gap edge are denoted 'GAP'and trees in or beneath the closed forest canopy are denoted 'FOR'. 'GAP' and 'FOR' are also used as subscripts to indicate the position of SUB and CAN trees. Tree position relative to the gap was based on field observations, crown maps and on simulations of light for each tree crown using the spatially explicit light model tRAYci (Brunner 1998). This model was run with a spatial resolution (3D) of 0.2 m for tree crowns predicting light (Percentage Above Canopy Light, PACL) for approximately 100 points on every crown using a high sample ray resolution. When ranking trees according to their maximum PACL the results were in accordance with field observations. Table 2 provides an overview of the trees and their classification.

In the first analysis, differences among groups during the measurement period were tested for differences in the monthly means of $J_{s\text{-}sum}$, $J_{s\text{-}max}$, E_{sum} and E_{max} (t-test, $p<0.05$). Preliminary analyses showed that there were no significant differences between the groups CAN_{GAP} and CAN_{FOR} and in the second analysis, the effect of low SWC on mean $J_{s\text{-}sum}$ for each of the beech groups CAN, SUB_{FOR} and SUB_{GAP} was tested in a non-linear regression model with D_{mean} and R_g:

Eq. (2) $$J_{s-sum} = (k_1 + k_2 \cdot \ln(D_{mean})) \cdot \exp(\frac{a}{R_g})$$

Where k_1, k_2 and a are fitted parameters, D_{mean} is the daily mean D in daylight hours (PPF > 10 µmol m^{-2} s^{-1}) and R_g is global radiation (J m^{-2} day^{-1}). The part of Eq. (2) including D_{mean} has been used in other studies (Oren and Pataki 2001, Hölscher et al. 2005) and the part including R_g displays a hyperbolic curve for $a <$ 0 (Curtis 1967). In the preliminary analyses, a number of models were tested, differing primarily in their representation of R_g being either linear (R_g / maximum R_g) or saturating (exp(a/R_g). For the purpose of this study the model in Eq. (2) was chosen based on the homogeneity of variance and the resulting high adjusted R^2 -values (Weisberg 1985) across all the beech groups. A linear representation of R_g would have worked equally well for SUB_{FOR} and CAN groups. The relative SWC was defined as SWC_{REL} = (SWC - WP) / (FC - WP) (Granier et al. 2000a), where WP is the permanent wilting point, FC is the field capacity and SWC was the mean of 10 observations nearest the sample trees in or beneath the closed canopy. Eq. (2) was fitted for three levels of SWC_{REL}: dry (<0.45), intermediate (0.45-0.60) and moist (>0.6) conditions. The significance of the three-level-model was determined in an F-test (Weisberg 1985, $p < 0.05$). FC was determined in-situ as the mean SWC from January to April and WP was found for loose soil in the laboratory (Schjønning 1985, 4 vol.%) from four soil samples in each of four soil depths (Dalsgaard 2007). SWC was linearly interpolated between the biweekly observations when P=0. Observations of D_{mean} and R_g were available for 108 days and SWC for 59 days. D_{mean} was based on measurements in the forest. Preliminary analyses had shown that these were slightly closer related to transpiration than measurements from the field. D_{mean} in the forest and above the field ($D_{mean\text{-}FIELD}$) were closely related: $D_{mean\text{-}FIELD}$ = 1.13 D_{mean} + 0.48 (R^2 -value 0.94). Highest observed D_{max} was 22.3 hPa (forest) and 25.8 hPa (field) observed simultaneously on June 21 and the mean D for the measurement period was 3.3 hPa at the forest station and 3.8 hPa at the field station. Analyses were conducted using the GLM and NLIN procedures in SAS version 8.1 and 8.2 (SAS Institute, Cary, NC).

Results

Measurements in 2001

Meteorology and soil water content

In July 5-12, 2001, the first four days were fine summer days, July 9 was dominated by approaching thunderstorms and generally overcast, July 10-12 were partly overcast and precipitation occurred in the evening or early morning hours (Figure 2e). Daily maximum T_a in the forest was 17-27 °C (maximum observed T_a was 28 °C at the open-field station) and SWC was 13-15 vol.%.

Radial variation in sap flow

Measurements of J_s were high for the first four days of the measurement period. J_s was low on July 9 and variable on July 10-12 reflecting variations in PPF and D (Figure 2a-d). For three of the four trees (Figure 2b-d) $J_{s0\text{-}20}$ was higher than $J_{s20\text{-}40}$ and $J_{s40\text{-}60}$. In one tree (Figure 2a) $J_{s20\text{-}40}$ was higher than observations in the two other depths. The radial profile differed among trees and changed in the diurnal time resolution according to the evaporative demand (Figure 3) though no general pattern emerged for all four trees. In two trees (Figure 3b-c) the profile tends to be steeper at low than at high evaporative demand, and in one tree (Figure 3a) the opposite was observed. The resulting profile found by fitting Eq. (1) to observations, shows a decrease in J_s with increasing xylem depth (Figure 4).

Measurements in 2000

Meteorology and soil water content

The summer of 2000 was characterized by frequent rain and a low D_{mean} (6-7 hPa) except for a short period around June 20 where D_{mean} was near 12 hPa (Figure 5b). Precipitation during the measurement period was 212 mm, which is close to the 30-year mean. Individual measurements of SWC below the closed canopy reached values down to 10 and 8 vol.% (approximately -0.5 and -0.6 MPa) in late July and late August respectively. SWC was higher in the gap than below the closed canopy throughout the measurement period (Figure 5c). Mean and highest

observed T_a was 14.5°C and 28.9°C at the forest station and 14.8°C and 30.8°C at the field station.

Sap flow variation among individual trees

The mean of $J_{s\text{-}sum}$ or $J_{s\text{-}max}$ for each tree for the entire measurement period did not vary significantly with stem diameter or tree height for either ash or beech (Figure 6). For beech, mean E_{sum} apparently increased with both stem diameter and height, but the relationships were not significant though the increase with tree height was near-significant (p=0.06). Observations for the largest tree in the sample (stem diameter 0.7 m) were low.

Temporal variation in sap flow

Preliminary analyses for beech showed that CAN_{FOR} and CAN_{GAP} did not differ and the following comparisons are presented below, i) three levels describing tree size and position (CAN, SUB_{FOR}, $SUB_{GAP)}$, ii) two levels describing tree size (CAN, SUB), and iii) two levels describing tree position relative to the gap (GAP, FOR). Further, for ash the effect of tree position was tested (GAP, FOR) and the difference between ash and beech were tested.

Late in the growing season there was a clear effect on sap flow of tree position relative to the gap for all trees in the sample as well as for subcanopy trees. Mean monthly $J_{s\text{-}sum}$ and $J_{s\text{-}max}$ in beech were similar for CAN, SUB_{GAP} and SUB_{FOR} in June (Table 3). In Table 3 different letters within the same month indicates significant differences among groups. In September $J_{s\text{-}sum}$ and $J_{s\text{-}max}$ for SUB_{FOR} was significantly lower than SUB_{GAP} and values had decreased to 55% ($J_{s\text{-}sum}$) and 51% ($J_{s\text{-}max}$) of the values for SUB_{GAP}. Figure 5a shows $J_{s\text{-}sum}$ during the measurement period. When contrasting GAP and FOR (results not shown), differences in $J_{s\text{-}sum}$ were significant in September (p = 0.043) and for $J_{s\text{-}max}$ differences were significant in August (p = 0.027) and September (p = 0.025). There was no effect on sap flow of tree size alone as no significant differences in $J_{s\text{-}sum}$ or $J_{s\text{-}max}$ were found when contrasting CAN and SUB (results not shown). $J_{s\text{-}sum}$ and $J_{s\text{-}max}$ were significantly lower in ash than in beech (Table 4). For ash, no effects were found of tree position relative to the gap.

The mean monthly E_{sum} in beech (Table 3) was significantly higher for CAN than SUB_{FOR} in July and August. In July and August SUB_{FOR} was 57 and 56% of CAN respectively. When contrasting E_{sum} for different tree sizes (CAN, SUB; results not shown), CAN showed significantly higher E_{sum} than SUB for June (p = 0.028), July (p = 0.027) and August (p = 0.043). No significant differences were found when contrasting E_{sum} for trees differing in position relative to the gap (GAP, FOR) and no significant differences were found from the analyses of E_{max}.

In early summer, CAN, SUB_{GAP} and SUB_{FOR} for beech showed similar diurnal J_s (Figure 7a) but differences developed toward the end of the measurement period. On a clear day, June 21, where SWC was high, differences among groups were small. SUB_{FOR} showed a slightly higher maximum than CAN and SUB_{GAP} and both SUB_{GAP} and SUB_{FOR} had a sharper decrease in afternoon J_s than CAN. After the sunny period around June 20, no more clear days were recorded. This made it difficult to compare diurnal curves of J_s over time. On a slightly overcast day, July 13, where SWC was high, trees are ranked similarly as on June 21. On a slightly overcast day, August 23, where SWC was low SUB_{GAP} shows a J_s higher than both CAN and SUB_{FOR}. For ash (Figure 7b) the diurnal course of J_s is shown for trees in the closed forest (FOR) and trees near the gap (GAP) for the same days as in Figure 7a. The mean J_s for GAP indicate that trees may have been able to sustain high J_s compared to FOR. However, the variation among GAP trees is large.

Nonlinear regressions showed, that $J_{s\text{-}sum}$ was well represented by Eq. (2) including only D and R_g (n=108). For SUB_{FOR}, SUB_{GAP} and CAN R^2 -values were 0.88, 0.90 and 0.91 respectively. When including parameters for each of three levels of SWC_{REL} in the model (n=59) these were significant (p<0.001) for SUB_{FOR} (F-value 12.1) and CAN (F-value 8.8), but not for SUB_{GAP}.(F-value 2.0; p> 0.05). For SUB_{FOR}, SUB_{GAP} and CAN R^2 -values were 0.94, 0.88 and 0.93 respectively. To illustrate the significant differences $J_{s\text{-}sum}$ was predicted for high and low evaporative demand at dry and moist soil water conditions respectively (Table 5). For SUB_{FOR} predicted $J_{s\text{-}sum}$ in dry conditions was 62-64% of $J_{s\text{-}sum}$ in moist conditions. For CAN predicted $J_{s\text{-}sum}$ in dry conditions was 61-71% of $J_{s\text{-}sum}$ in moist conditions. Figure 8 illustrates the effect of low SWC_{REL} on $J_{s\text{-}sum}$.

Discussion

In the present study, sap flow measurements in beech and ash from trees near a canopy gap in a deciduous beech dominated natural forest reserve were presented. The results document the differences in J_s and E that emerged through the growing season 2000 among beech trees in different canopy layers and proximity to the canopy gap as well as the decrease in J_s with increasing xylem depth in beech.

Radial variability in J_s

The radial variation in J_s observed for beech was characterized by a decrease with increasing xylem depth. This is in agreement with other studies of the radial variability in J_s for this species. It confirms that consideration of the radial variation is necessary to avoid an overestimation of transpiration compared to the alternative of using sap wood area to calculate tree transpiration (Geβler et al. 2005, Lüttschwager and Remus 2007). Measurements represented mature trees within a narrow range of stem diameter (0.35-0.42 m) and tree height (25-27 m) relative to the wide range in the stand as a whole. Despite of these similarities the four trees showed different radial variations with examples of a strongly decreasing J_s with xylem depth (Figure 2d), a moderate decrease in J_s (Figure 2c) and an initial increase in J_s followed by a decrease (Figure 2a). A similar radial variation of J_s in trees of similar stem diameter as suggested by Lüttschwager and Remus (2007) does not seem to be indicated in the present study. However, these authors measured in an even-aged stand (117 years). The trees in the present study possibly differed in age and may therefore not conform to the characteristics of the data on which the model of Lüttschwager and Remus (2007) was developed. The radial decrease with depth observed in the present study was moderate compared to observations in several other studies (Figure 4, Granier et al. 2000a, Schäfer et al. 2000, Köstner et al. 1998, Lüttschwager and Remus 2007). Slightly increasing J_s with xylem depth (Lang 1999, Lüttschwager and Remus 2007) or a similar J_s among xylem depths to a depth of 60 mm (Geβler et al. 2005) have been observed in other studies predominantly on large or open grown trees. Differences in the radial profiles in J_s in the present study may be due to differences in rooting depth. Nadezhdina and Čermák (2003) showed that shallow roots supplied water predominantly to the outer xylem and to leaves exposed to the sun and deep roots supplied water to the inner xylem or to the entire xylem. Other factors influencing

the radial profiles may be stem increment (Lüttschwager and Remus 2007) or embolism following frost (Lemoine et al. 1999) causing a decrease in xylem hydraulic conductivity in the stem resulting in low sap flow in deep compared to the outermost xylem.

Variability in J_s due to tree size and position relative to canopy gap

It was confirmed that sap flow for canopy trees and for subcanopy trees beneath the canopy was limited by low soil water content following the progression of a seasonal soil drought. In contrast the sap flow of subcanopy trees near the canopy gap was unaffected by drought. The growing season of 2000 was not particularly dry or hot. Even so, SWC_{REL} beneath the closed forest decreased to a level of approximately 0.4 where beech canopy conductance has been shown to be limited relative to its potential (Granier 2000a). Effects on sap flow of competition for soil water was also observed by Vincke et al. (2005) where sap flow was higher in thinned than in unthinned *Quercus robur* (L.). Further, in *Pinus sylvestris* (L.) trees at the forest edge had a higher sap flow rate than trees in the interior of the stand (Cienciala et al. 2002).

In the present study, the mean monthly $J_{s\text{-}sum}$ did not differ between canopy trees and subcanopy trees beneath the canopy as hypothesized. But the lower mean monthly E_{sum} in July and August for subcanopy than canopy trees indicate that transpiration is progressively more limited for trees below than in the canopy. Suppressed trees of beech may have a relatively large crown projected area to maximize the interception of radiation in their generally shaded position which could be a reason why significant differences were found for calculated E_{sum} and not for $J_{s\text{-}sum}$. Other studies have found that deeper rooting of large than small *Acer saccharum* (Marsh.) trees caused a higher transpiration in large trees and a lower sensibility to decreasing soil water content (Dawson 1996). The growth of small beech trees was more sensitive to drought than large trees (Piutti and Cescatti 1997). In the study of Lüttschwager and Remus (2007), the radial profiles in J_s differed among trees of different diameter with large trees showing the most moderate decrease with increasing xylem depth. This may indirectly indicate that large and dominant trees tend to have deep roots with access to a large volume of soil (Nadezhdina and Čermák 2003).

Growing season mean of $J_{s\text{-}sum}$ and $J_{s\text{-}max}$ did not increase systematically with tree size which was expected based on observations from Granier (2000a). Simpson (2000) and Barbour and Whitehead (2003) found that sap flow rates did not vary significantly with tree stem diameter (up to approximately 0.7 m) in heterogeneous coniferous stands. Though variability was large mean E_{sum} in the present study generally increased with increasing tree height (near-significant relationship in beech). In *Nothofagus* Köstner et al. (1992) found that emergent trees had a larger transpiration pr. crown area than subdominant and suppressed trees. Sap flow for the largest tree in the sample in the present study (diameter 0.7 m) was low. Whether this was due to effects of age (Delzon and Loustau 2005) or low vitality (Vincke et al. 2005) could not be resolved in the present study. Low stomatal conductance has been observed for tall beech trees (Schäfer et al. 2000). Studies at the same site as the present study (Dalsgaard 2007, Dalsgaard, Mikkelsen and Bastrup-Birk, subm.) indicate that tree height does not limit transpiration in this forest which is also supported by results in Granier et al. (2000a) and Köstner (2001).

Methodological considerations

Monthly mean $J_{s\text{-}sum}$ for ash was significantly lower than for beech. Most likely the sap flow probes were placed partly in inactive xylem. Steep gradients in J_s within the length of the probe result in an underestimation of J_s (Clearwater et al. 1999). Adjusting J_s according to Clearwater et al. (1999) assuming that water is conducted primarily in the outer 10 mm of the xylem in ash (Hölscher et al. 2005) results in a three-fold increase in the daily maximum J_s (Dalsgaard 2007). Hölscher et al. (2005) found that ash had very low sap flow rates (daily integrated sap flow rates were approximately 50% of the rates observed for beech) partly due to low ash leaf area. The measurements in ash in the present study are assumed to be influenced by the placement of the probes reaching into inactive xylem and therefore not used in regression models or to estimate tree transpiration. Low leaf area for ash probably also contributed to the low measured J_s but this was not quantified in this study. Stöhr and Lösch (2004) found sap flow rates of ash saplings to exceed the rates observed in most other European tree species when expressed on a leaf area basis.

With one set of sap flow probes for each tree in the study in 2000 and for each tree and xylem depth in 2001, measurements are vulnerable to spatial variability

in J_s. However, measuring in beech, Schäfer et al. (2000) was able to show expected relationships between sap flow and tree size based on one or a few sensors in each of nine trees. While more sensors for each tree and more trees in the sample in the present study would have been beneficial, using group averages of J_s should cover some of the spatial variability. Observations in mature beech indicated that J_s did not vary with aspect (Mikkelsen, unpubl.) thus installing probes in the northern side of stems should not have introduced any systematic errors.

Possible implications for forest dynamics

Results indicate that in beech forests characterized by small scale disturbance beech trees at the edge of a canopy gap benefit from the high availability of soil water during periods of progressive soil drought. This is supported by the observation that soil water content gradually decreased at the edges of the canopy gap during the growing season while values near field capacity were maintained in the gap centre (Ritter et al. 2005). Further, high water use by edge trees could be inferred from the estimation of gap and closed forest water balance (Dalsgaard, Bastrup-Birk, Schelde and Raulund-Rasmussen, subm.). Branch hydraulic architecture in recently thinned trees acclimates to increased levels of light by developing a higher hydraulic conductivity and xylem safety relative to cavitation (Lemoine et al. 2002). This reduces any hydraulic limitations to carbon assimilation (Maherali et al. 1997). It is suggested that when subcanopy trees are released following gap formation they are able to take advantage of the increase in light interception because of high soil water availability. This possibly results in a high growth rate for trees at the edge of canopy gaps (Catovsky et al. 2002) and contributes to the crown expansion observed in edge trees (Hibbs 1982, Muth and Bazzaz 2002). High soil water availability may result in high rates of gap closure. Further, soil conditions influencing tree water availability as for example soil hydraulic conductivity (Čermák and Prax, 2001) water holding capacity (Vilhar et al. 2005) and competition with ground vegetation (McGuire et al. 2001) may affect the rate of gap closure and thereby forest dynamics.

Conclusions

The seasonal development in sap flow and transpiration was shown for trees according to their size, species and position relative to the gap. It was confirmed

that seasonal soil drought limits sap flow for beech trees in the closed forest but not those at the gap edge. This was illustrated for subcanopy trees (height < 20 m) among which mean $J_{s\text{-}sum}$ was similar in June but by September suppressed trees showed a significantly lower value of approximately 55% relative to released trees near the gap. Further, regression analyses showed that $J_{s\text{-}sum}$ was significantly reduced (by 29-39%) for canopy trees and for subcanopy trees in the closed forest with the progression of soil drought in contrast to released subcanopy trees at the gap edge. Sap flow was similar for trees in and beneath the closed forest canopy, but transpiration relative to the crown projected area was lower for suppressed than for canopy trees in July and August, approximately 55%, indicating that they were possibly limited by soil drought to a larger degree than canopy trees. It is suggested that processes affecting tree water uptake from a canopy gap may influence the growth rates for edge trees and thereby the rate of gap closure and forest dynamics. A simple model of the radial variation in sap flow for beech was estimated from four trees to a depth of 60 mm and used in the calculation of beech transpiration. Sap flow decreased with increasing xylem depth, but the decline was less steep than in many other studies. Possibly this model is specific for the natural forest site used in this study. The age, stem increment and rooting depth of the sample trees could have influenced the resulting model. Sap flow measurements in ash were low. Measurement were assumed to have been influenced by the use of probes (20 mm) reaching beyond the xylem active in water transport, but low leaf area may also have influenced sap flow.

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Tables

Table 1. Parameters describing stand structure in Suserup Forest, a beech dominated natural forest reserve in Denmark. Stand top height is the mean height of the tallest 100 trees ha^{-1}.

Basal area (m^2 ha^{-1})	40.2
Stand density (trees ha^{-1})	733
Mean tree height (m)	13.3
Stand top height (m)	28.4
Mean stem diameter (m)	0.18
1st quartile, diameter (m)	0.07
3rd quartile, diameter (m)	0.23
Stand leaf area index (m^2 m^{-2})	4.6[b]
Tree species	*Fagus sylvatica* L. (56)
(% of stand basal area)	*Fraxinus excelsior* L. (28)
	Quercus robur L. (13)
	Ulmus glabra Huds. (3)

[b] Measured August 24-25, 2000 with the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA).

Table 2. Tree height (H), stem diameter (SD) and crown projection area (CP) for trees sampled in 2000 for sap flow in Suserup Forest, Denmark. Four trees (×) were sampled in 2001 for measurements of radial variation in sap flow. Canopy layer and the position relative to a small canopy gap are shown along with an index of crown exposure ($PACL_{max}$, Maximum Percentage Above Canopy Light) computed using the spatially explicit light model tRAYci.

Tree no.	Species	H (m)	SD (m)	CP (m^2)	Canopy layer and position[3]	$PACL_{max}$ (%)
15	*F. sylvatica*	14.2	0.11	9.0	SUB_{FOR}	21.2
10	*F. sylvatica*	15.4	0.11	20.4	SUB_{FOR}	23.7
18	*F. sylvatica*	18.1	0.17	20.3	SUB_{FOR}	29.1
7	*F. sylvatica*	16.0	0.19	27.4	SUB_{GAP}	39.4
8	*F. sylvatica*	18.9	0.21	51.5	SUB_{GAP}	68.9
11	*F. sylvatica*	19.8	0.22	42.1	SUB_{GAP}	76.7
12[2] ×	*F. sylvatica*	25.5	0.37	74.3	CAN_{FOR}	47.6
20[1] ×	*F. sylvatica*	24.9	0.42	86.1	CAN_{FOR}	83.5
13	*F. sylvatica*	29.0	0.70	122.3	CAN_{FOR}	94.7
17 ×	*F. sylvatica*	26.8	0.35	59.7	CAN_{GAP}	89.4
19 ×	*F. sylvatica*	25.5	0.37	47.1	CAN_{GAP}	90.9
14	*F. sylvatica*	27.6	0.50	80.0	CAN_{GAP}	94.3
1	*F. excelsior*	31.1	0.33	30.7	CAN_{GAP}	99.0
2	*F. excelsior*	26.8	0.31	30.7	CAN_{GAP}	92.7
3	*F. excelsior*	27.0	0.38	71.8	CAN_{FOR}	72.4
5	*F. excelsior*	26.0	0.33	30.8	CAN_{FOR}	91.1
6	*F. excelsior*	33.7	0.70	145.1	CAN_{FOR}	99.9
4	*F. excelsior*	19.1	0.22	29.0	SUB_{FOR}	24.6

[1] Due to technical errors measurements in 2000 of this tree ceased on July 21.

[2] Near an over 30 m tall ash tree.

[3] SUB = subcanopy trees, CAN = canopy trees, subscript 'GAP' denotes a position near the gap, subscript 'FOR' denotes a position in or beneath the closed canopy.

Table 3. Monthly mean values for beech of $J_{s\text{-}sum}$ (daily sum of J_s), $J_{s\text{-}max}$ (daily maximum J_s) and E_{sum} (daily transpiration) for subcanopy trees near the gap (SUB_{GAP}), subcanopy trees below the canopy (SUB_{FOR}) and canopy trees (CAN), in Suserup Forest, Denmark June 15 - September 30, 2000. Different letters within for the same month and response variable indicate significant differences ($p<0.05$) in *t*-test. The standard error of the mean is shown in parenthesis.

	June	July	August	September
$J_{s\text{-}sum}$ (kg m^{-2} day^{-1})				
SUB_{GAP}	^{A}1055 (126)	^{A}996 (130)	^{A}1022 (134)	^{A}748 (101)
SUB_{FOR}	^{A}1056 (49)	^{A}745 (86)	^{A}690 (82)	^{B}410 (49)
CAN	^{A}1201 (131)	^{A}1056 (136)	^{A}968 (108)	^{AB}637 (88)
$J_{s\text{-}max}$ (g m^{-2} s^{-1})				
SUB_{GAP}	^{A}41.2 (4.4)	^{A}41.9(5.8)	^{A}43.3(6.0)	^{A}36.4(5.1)
SUB_{FOR}	^{A}40.7(1.6)	^{A}30.6(3.8)	^{A}27.8(4.0)	^{B}18.7(2.8)
CAN	^{A}40.5(3.7)	^{A}38.9(4.2)	^{A}38.7(4.3)	^{AB}29.3(4.1)
E_{sum} (mm day^{-1})				
SUB_{GAP}	^{A}0.62 (0.10)	^{AB}0.59 (0.10)	^{AB}0.60 (0.10)	^{A}0.44 (0.08)
SUB_{FOR}	^{A}0.70 (0.17)	^{A}0.50 (0.14)	^{A}0.47 (0.14)	^{A}0.28 (0.08)
CAN	^{A}1.00 (0.09)	^{B}0.87 (0.09)	^{B}0.84 (0.10)	^{A}0.55 (0.09)

Table 4. Monthly mean values of $J_{s\text{-}sum}$ (daily sum of J_s) and $J_{s\text{-}max}$ (daily maximum J_s) for ash and beech in Suserup Forest, Denmark June 15 - September 30, 2000. Different letters within for the same month and response variable indicate significant differences ($p<0.05$) in *t*-test. The standard error of the mean is shown in parenthesis. The table shows the original data but the test was based on ln-transformed data.

	June	July	August	September
$J_{s\text{-}sum}$ (kg m^{-2} day^{-1})				
F. excelsior	^{A}413 (50)	^{A}399 (42)	^{A}442 (62)	^{A}331 (45)
F. sylvatica	^{B}1128 (72)	^{B}965 (82)	^{B}907 (73)	^{B}605 (61)
$J_{s\text{-}max}$ (g m^{-2} s^{-1})				
F. excelsior	^{A}10.7(1.3)	^{A}10.7(1.1)	^{A}11.9(1.7)	^{A}9.6(1.4)
F. sylvatica	^{B}40.7(2.0)	^{B}37.6(2.8)	^{B}37.0(3.1)	^{B}28.1(3.0)

Table 5. Predicted values of $J_{s\text{-}sum}$ (kg m^{-2} day^{-1}) for the beech groups SUB_{FOR} and CAN in low and high evaporative demand and in dry ($SWC_{REL} < 0.45$) and moist ($SWC_{REL} > 0.6$) soil water conditions. Model: $J_{s\text{-}sum} = (k_1 + k_2 \cdot \ln(D_{mean})) \cdot \exp(a / R_g)$ where D_{mean} is the daily mean vapour pressure deficit in daylight hours and R_g is global radiation. For SUB_{FOR} parameter values were: $k_1 = 774.7$, $k_2 = 254.0$, $a = -6327995$ (dry) and $k_1 = 1118.3$, $k_2 = 540.7$, $a = -4802988$ (moist). For CAN parameter values were: $k_1 = 1088.5$, $k_2 = 255.3$, $a = -7342559$ (dry) and $k_1 = 1254.3$, $k_2 = 538.6$, $a = -3358430$ (moist). Parameters were found from input in kPa and J m^{-2} day^{-1} and predictions were multiplied by a unit conversion factor of 1.8.

	low		high	
R_g	10 MJ m^{-2} day^{-1}		20 MJ m^{-2} day^{-1}	
D_{mean}	6 hPa		10 hPa	
	dry	moist	dry	moist
SUB_{FOR}	686.73	1111.64	1016.24	1583.20
CAN	891.27	1459.96	1357.25	1908.74

Figures

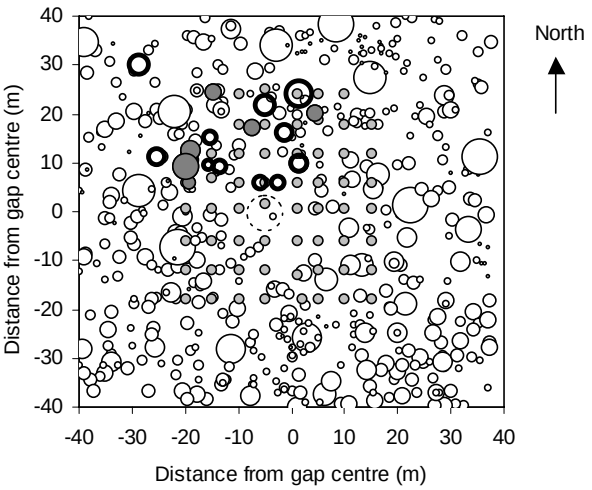

Figure 1. Overview of the measurement site in Suserup Forest. Small grey circles show the position of the SWC measurements and circles show the relative size and position of all trees. Sample trees selected for sap flow measurements are: dark gray circles (ash) and black lined circles (beech). A large tree near the gap centre is indicated with a thin dotted line. This tree lost most of its crown in a hurricane in December 1999 when the gap was formed.

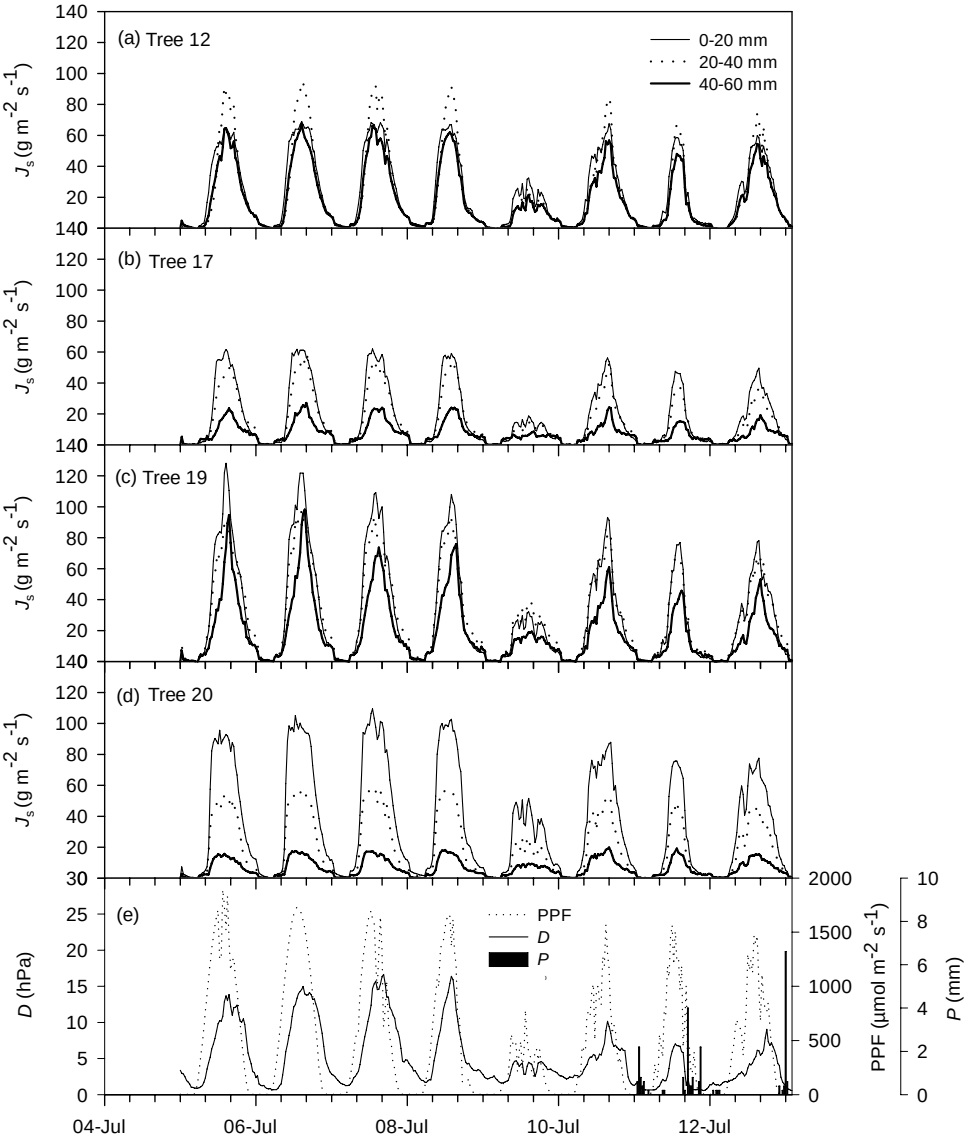
(a) Tree 12
0-20 mm
20-40 mm
40-60 mm
(b) Tree 17
(c) Tree 19
(d) Tree 20
(e)
PPF
D
P
Js (g m-2 s-1)
D (hPa)
PPF (µmol m-2 s-1)
P (mm)
04-Jul
06-Jul
08-Jul
10-Jul
12-Jul

Figure 2: (a) – (d): Diurnal course of sap flow (J_s) in three xylem depths of four beech trees and (e) vapour pressure deficit (D), photosynthetic photon flux (PPF) and precipitation (P). Observations from Suserup Forest, Denmark in July 2001.

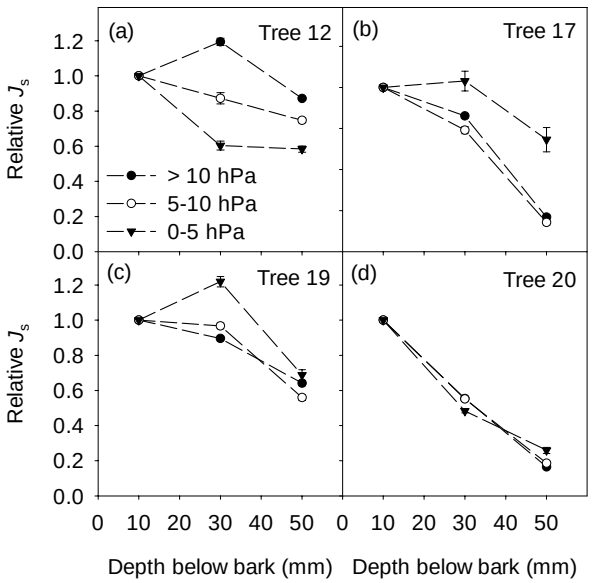

Figure 3: The relative sap flow (J_s) for 30-min observations in three xylem depths of four beech trees (J_s in 0-20 mm depth is unity). Averages are shown for three levels of D: 0-5 hPa (n = 80), 5-10 hPa (n = 66) and >10 hPa (n = 64). Error bars show ± one standard error of the mean. Measured July 5-12, 2001 in Suserup Forest, Denmark.

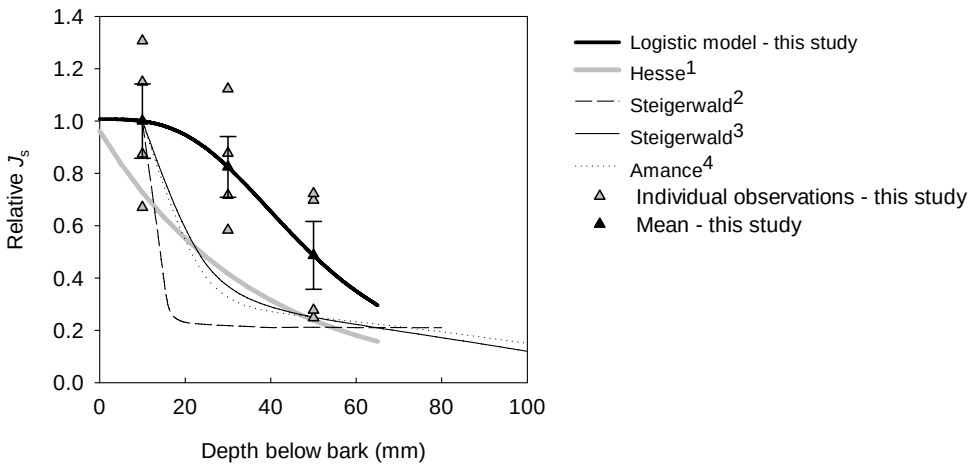

Figure 4. Radial variation in sap flow (J_s) of beech. [1] Granier et al. 2000a (3 trees), [2] Schäfer et al. 2000 (9 trees), [3] Schäfer and Köstner in: Köstner et al. 1998 (7 trees), [4] Granier in: Köstner et al. 1998 (1 tree). For Suserup and Hesse curves represent fitted models, for the remaining examples curves were estimated from graphs. For this study, observations were from four trees on July 5-12, 2001, Suserup Forest in Denmark. Error bars show ± one standard error of the mean. The predicted relative J_s from this study using a logistic model was: $y = a / [1+(x/x_0)^b]$ where the fitted parameters were: a: 1.0075, b: 3.0836, x_0: 4.8896.

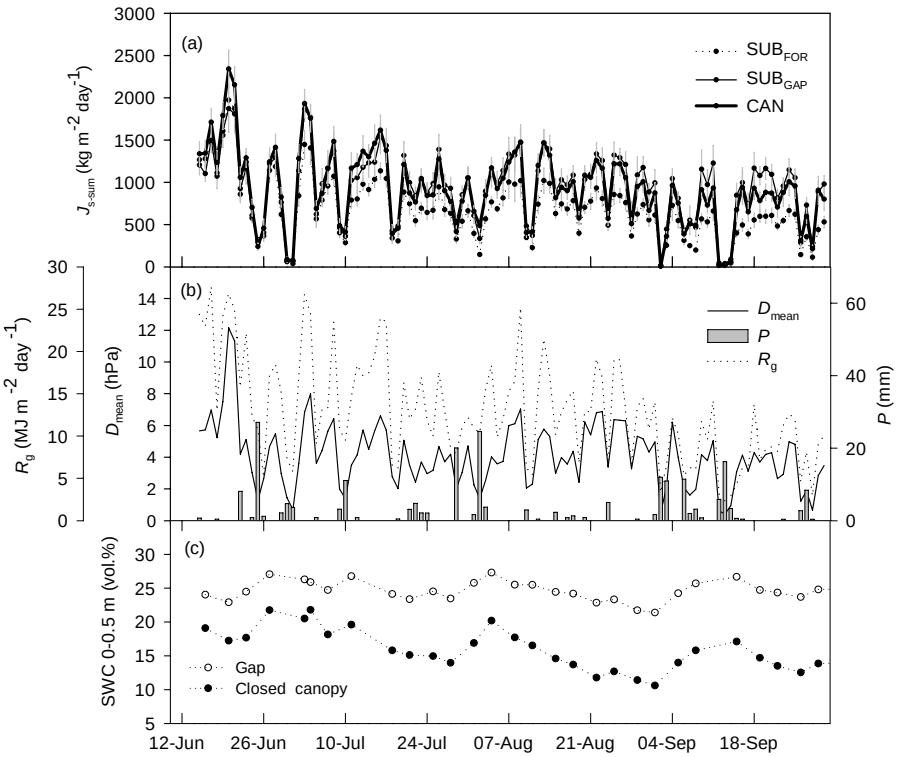

Figure 5. (a) Mean $J_{s\text{-}sum}$ for beech; CAN (n=6), SUB_{FOR} (n=3) and SUB_{GAP} (n=3). Error bars show ± one standard error of the mean. (b) Daily mean vapour pressure deficit (D_{mean}), global radiation (R_g) and precipitation (P). (d) Soil water content (SWC) in gap and below the closed forest canopy. Measurements obtained June 15 – September 30, 2000 in Suserup Forest, Denmark.

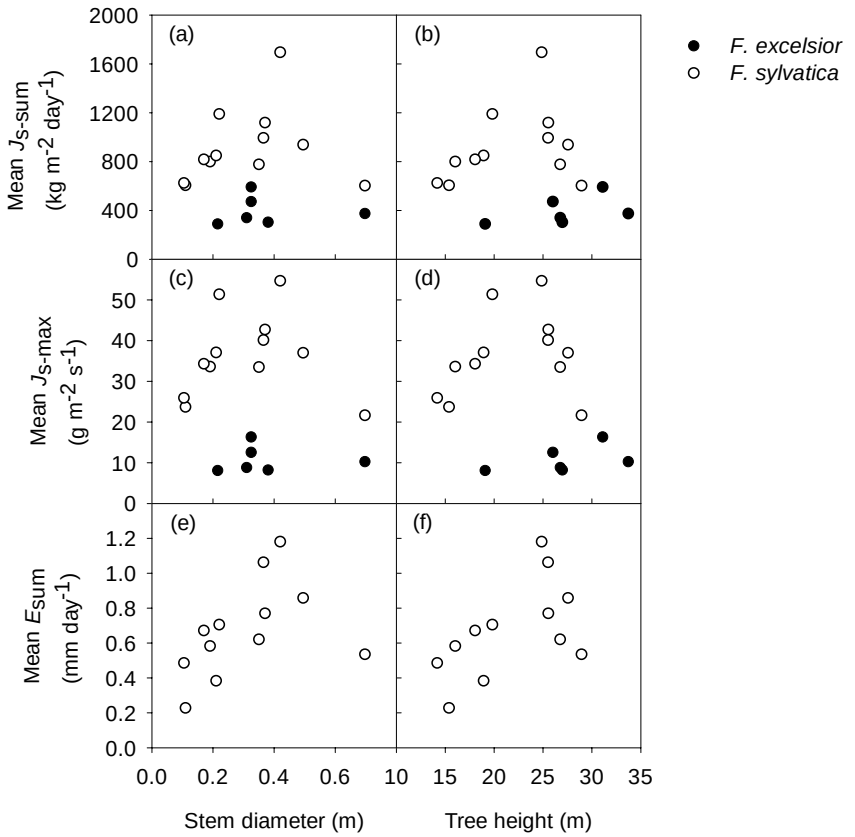

Figure 6. Mean for the study period of (a)-(b) $J_{s\text{-}sum}$, (c)-(d) $J_{s\text{-}max}$ and (e)-(f) E_{sum} related to stem diameter and tree height. The increase in E_{sum} with stem diameter and height (e)-(f) was not significant: (e) R^2 –value 0.19, p=0.16, (f) R^2 –value 0.31, p=0.06. Measurements from June 15 – September 30, 2000 in Suserup Forest, Denmark.

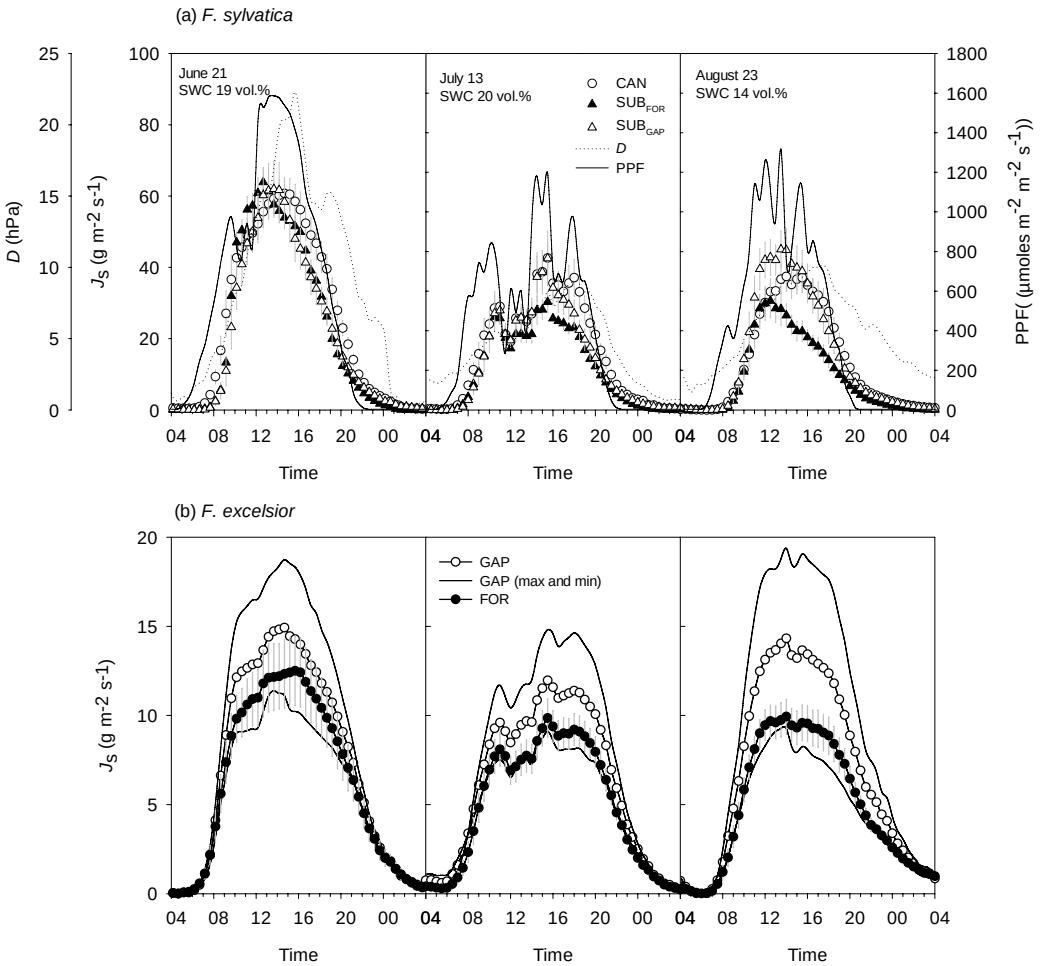
(a) F. sylvatica
June 21
SWC 19 vol.%
July 13
SWC 20 vol.%
August 23
SWC 14 vol.%
CAN
SUB_FOR
SUB_GAP
D
PPF
D (hPa)
J_S (g m-2 s-1)
PPF(µmoles m-2 s-1))
Time
(b) F. excelsior
GAP
GAP (max and min)
FOR
J_S (g m-2 s-1)
Time

Figure 7. Sapflow (J_s), radiation (PPF) and vapour pressure deficit (D) on three days measured in Suserup Forests, Denmark, 2000 for (a) beech (CAN, SUB_{GAP}, SUB_{FOR}) and, (b) ash, where the mean for trees in the closed forest (FOR) and near the canopy gap (GAP) is shown along with the maximum and minimum observations for GAP. Error bars show ± one standard error of the mean. Selected days represent a warm and sunny day with high soil moisture (June 21) and two partly cloudy days with high (July 13) and low (August 23) soil moisture respectively. Note different scales for J_s in (a) and (b).

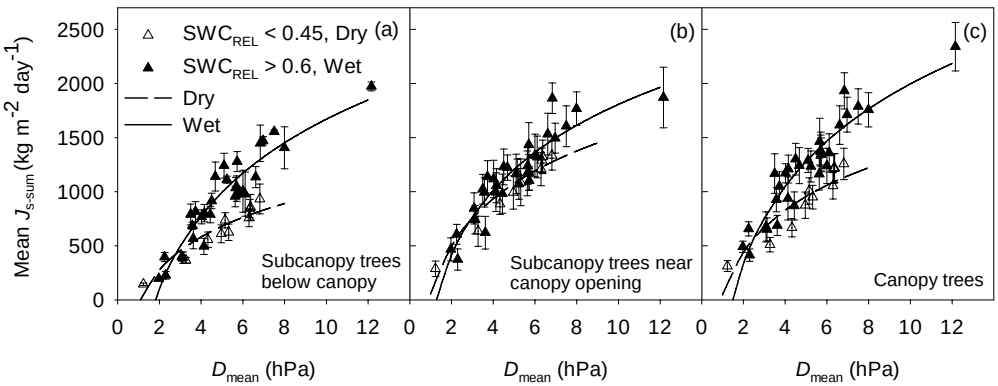

Figure 8. Mean $J_{s\text{-}sum}$ for the beech tree groups CAN, SUB_{FOR} and SUB_{GAP} relative to the daily mean vapour pressure deficit (D_{mean}) for high and low soil moisture. Measurements are from Suserup Forest, June 15 - September 30, 2000. Error bars show ± one standard error of the mean. To illustrate differences between dry and moist soil conditions curves were fitted for the model $J_{s\text{-}sum} = a + b \ln(D_{mean})$ in threes ranges of SWC_{REL} defined as in the text. The models resulted in R^2 –values of 0.88 (SUB_{FOR}), 0.85 (SUB_{GAP}) and 0.87 (CAN).

Paper IV

Transpiration and canopy conductance of European beech (Fagus sylvatica L.) in a natural and a mature managed stand

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Abstract

European beech (Fagus sylvatica L.) is an important species in natural and managed forests in Europe. Objectives of this study were to compare European beech transpiration (E) and canopy conductance (g_c) in a managed mature even-aged stand (MAN) and a nearby natural forest reserve (NAT) using simultaneous sap flow measurements. We hypothesized that the differences in height distribution between sites would influence g_c as well as the individual tree leaf level conductance (g_{Ltree}) due to a lower hydraulic conductance in tall trees, specifically that i) g_c in NAT is more sensitive to the air vapour pressure deficit (D) than in MAN, and ii) g_{Ltree} in NAT decreases with increasing tree height. Results showed that the sensitivity of g_c to D was similar between sites and that estimated g_{Ltree} was unrelated to tree height. Daily E in NAT was generally 80% of E in MAN in spite of similar plot basal area. Diurnal E was generally lower in NAT than in MAN but at high transpiration rates, the diurnal E was similar between sites. E in MAN correlated more strongly with D than with light. In NAT these correlations ranked opposite. For individual trees E was closer correlated to D for tall than for small trees. For diurnal E, a delay was observed at low light in NAT relative to MAN. While tree height did not influence transpiration we suggest that European beech E in MAN may experience a more pronounced limitation in the root-shoot pathway than in NAT.

Keywords: canopy structure, natural forest, sap flow, transpiration, tree height

Introduction

European beech (Fagus sylvatica L.) is a key species in both natural and managed forests in Northern Europe. To sustain important biological functions in managed forests (i.e. biodiversity), stand structures resembling those of natural forests are promoted. That is, a heterogeneous canopy structure characterized by a large range in tree height and diameter, a mixture in canopy species and occurrence of canopy gaps (Emborg et al. 2000). To understand the relationships between structure and function and thereby the hydrological processes in forest landscapes, it is relevant to investigate the main controls of the transpiration in such heterogeneous canopies (Köstner 2001). This study concerns the role of canopy structure in the regulation of transpiration for European beech. Most studies have been performed in even-aged stands (i.e. Herbst 1995, Magnani et al. 1998, Granier et al. 2000a, Dellwik 2003). Studies have shown that maximum leaf transpiration (Köstner 2001) and canopy conductance (g_c) (Granier et al. 2000a) for European beech were independent of stand age and stand height. In other studies, however, stomatal conductance and its sensitivity to changes in the air vapour pressure deficit (D) decreased with increasing tree height (Ryan et al. 2000, Delzon et al. 2004, Addington et al. 2006), also for European beech in a structurally heterogeneous stand (Schäfer et al. 2000). This was explained by an increase in the soil-to-leaf flow path resistance with height due to a longer path length and the effect of gravity in combination with the maintenance of constant leaf water content (Oren et al. 1999). Following these results the transpiration from a stand may be influenced by the variation in tree height. This study compares simultaneous measurements of canopy transpiration in European beech in an even-aged, homogenous mature managed stand and a nearby European beech dominated natural forest reserve characterized by a heterogeneous structure and a wide range in tree height. Transpiration is calculated from measurements of sap flow and is compared between sites on the daily and on the diurnal time scale. It is hypothesized that i) the sensitivity of the canopy conductance to D is higher in the natural than in the managed stand and ii) the individual tree leaf level conductance decreases with increasing tree height. To isolate the canopy structure effects, the hypotheses are tested in periods with non-limiting soil water conditions.

Methods

Study sites

Suserup Forest (NAT) is a 19.2 ha uneven-aged mixed deciduous forest reserve (55°22´N, 11°34´E). The soil is a loamy till with pockets of sandy till (Inceptisol) developed from moraine deposits (Vejre and Emborg 1996, Ritter and Vesterdal 2006). Field capacity (0-0.9 m depth) was 25.4 vol.% (228 mm). The plot was on a well-drained plateau in the central part of the forest, 200 m northeast of a lake and 80 m from the northern forest edge. An irregularly shaped canopy opening (diameter 20 m) created in a hurricane in December 1999 added to the heterogeneity of the crown space. The relative distribution of European beech basal area to height groups (height interval (m): %) was: 4-10: 3.8, 10-16: 10.3, 16-22: 15.0, 22-28: 31.1, above 28: 39.7. The forest was protected since 1807 and now appears as a natural forest with European beech trees up to 300 years of age (Emborg et al. 2000, Hannon et al. 2000). The Soroe site, Lille Bøgeskov Forest (MAN), is an even-aged and homogenous mature 80-year old stand (55º29'N, 11º38'E). A tower allows meteorological measurements in up to 57 m height (Pilegaard et al. 2003). The soil (Mollisol) is rich in clay (8-23 %), field capacity (0-1.5 m depth) was 31.5 vol.% (473 mm) and the groundwater table fluctuates between 0.2 m in winter and 2 m in summer below the soil surface (Ladekarl et al. 2001). The two sites are 13 km apart, situated in the central part of Zealand, Denmark. Stand structure is described in Table 1. The mean annual air temperature is 8.1°C (1987-1997, Laursen et al. 1999). The mean annual precipitation (1961-1990, Frich et al. 1997) is 644 mm in NAT and 668 mm in MAN.

Meteorological and soil water content measurements

In NAT, two climate stations were established, one below the canopy and one above an open field 300 m from the forest site. They both measured the relative air humidity (RH, %) and air temperature (T_a,°C; Vaisala HMP45C, Helsinki, SF), and wind speed (u, $m \cdot s^{-1}$; Vector Instruments A100L2, Denbighshire, UK). In addition the open-field station measured precipitation (P, mm; Pronamic, Rain-o-matic, Silkeborg, DK) and photosynthetically active radiation (PPFD, $\mu mol \cdot m^{-2} \cdot s^{-1}$; Li-Cor LI190SA Quantum Sensor, Lincoln, NE). The stations measured 2 m above the ground, instruments were scanned every 10 seconds and averages

were calculated for every 30 min (DL2e (Delta-T Devices Ltd, Cambridge, UK) or DT50 (dataTaker Pty Ltd., Rowville, AU)). In MAN, measurements were RH (25 m = canopy surface; Vaisala HMP45A, Helsinki, SF), T_a (37 m; pt-100, Risø, DK), PPFD (57 m; instrument as in NAT), u (37 m; P2244, Risø, DK) and P (25 m; instrument as in NAT). Light sensors generally showed low values in NAT. When compared on moving 5 or 10-hour averages to measurements in MAN they showed 90 % of the values in June through July 2000 and values were adjusted to compare with those for MAN. Global radiation (R_g) was calculated from PPFD (Monteith and Unsworth 1990, Lambers et al. 1998). Air vapour pressure deficit (D) was calculated from RH and T_a (Buck 1981). D_{mean} is the daily mean D during daylight hours and D_{max} is the highest daily observation of D. The volumetric soil water content (SWC, vol.%) was measured in the closed forest using Time Domain Reflectometry (Topp et al. 1980) (Tektronix 1502C/1502B, Tektronix inc., Berkshire, UK). Stationary 0.5 m long probes were installed vertically from the soil surface. In NAT, measurements were manual and biweekly (n=10; Dalsgaard 2007a). In MAN they were automatic (every two hours, n=28) and adjusted based on gravimetric soil water content measurements (Ladekarl 2001). SWC was transformed to a measure of plant available soil water based on Granier et al. (2000a, b): SWC_{REL}= (SWC - wilting point) / (field capacity - wilting point)). Wilting point was 4 vol.% based on soil water retention analyses (Schjønning 1985, Dalsgaard 2007b, Ladekarl pers. comm.) and field capacity was determined in-situ (mean of measurements from January to April).

Sap flow

Sap flow was measured as the sap flux density (J_s, $g \cdot m^{-2} \cdot s^{-1}$) using the thermal dissipation technique (Granier 1985, 1987, Granier et al. 1996). At both sites, measurements were made every 60 seconds and averages were logged every 30 min. (NAT: DL2e, Delta-T Devices Ltd, Cambridge, UK and MAN: Campbell, CR7, Campbell Scientific, Logan, Utah, USA). Probes were 20 mm long and 2 mm in diameter (in NAT manufactured by ProBit, Germany). They were inserted radially into the northern side of the stem where the upper probe was heated by a constant current of 120 mA. J_s was calculated according to Granier (1985, 1987). The installations were protected from water intrusion by silicon paste, a plastic cover and insulating foam and from heating by direct sunlight by reflective blankets/aluminium foil. At both sites, sample trees were selected to represent the stand. In NAT, J_s was measured on 12 trees from June 15 – September 30, 2000

(installation in June 2000). The sample trees (see Table 2) were positioned north-west of the canopy opening. The relative distribution in the sample of European beech basal area to height groups (height interval (m): %) was: 10-16: 1.7, 16-22: 15.4, 22-28: 47.2, above 28: 35.7. For each tree one pair of probes were inserted 2 m above the ground (0-20 mm xylem depth) with a vertical distance of 0.2 m. Heat conducting paste was applied to the probes in a thin layer before installation (the upper heated sensor in an aluminium pipe). In MAN, J_s was measured on 12 trees (diameter 0.35-0.44 m) from May 5 – September 30, 2000 (installation in March 2000). All sample trees were in the canopy layer with a height of 25 m ± 1 m. For each tree 2 pairs of probes were inserted in two xylem depths (0-20 mm and 20-40 mm) 1.3 m above the ground with a vertical distance of 0.1-0.2 m.

Plot transpiration

Due to differences in stand structure and within-tree measurement resolution, scaling of J_s to plot transpiration (E) was not identical between sites. The best possible procedure was chosen for each site. To scale from sensor to tree in MAN, J_s in each of the two measurement depths were averaged. The flux deeper than 40 mm was approximated by assuming 20% of the outer (0-20 mm) flux in the xylem in 40-100 mm depth (Köstner et al. 1998, Granier et al. 2000a). J_s in each of the three xylem depths was combined into a weighed average. In NAT a model estimating the xylem area active in water transport was estimated from the measured radial variation in J_s in four of the sample trees in July 2001 (Dalsgaard 2007b, Dalsgaard in prep.). Relative $J_s = 1.0075 / (1 + (x / 4.8896)^{3.0836})$, where x is the depth (cm) and the relative J_s is J_s at a given depth relative to J_s measured in the outer 20 mm of the xylem.

While the canopy in MAN was single layered, closed and with little crown overlap, the canopy in NAT displayed significant crown overlap (layering) and variable canopy openness affected the seasonal course of individual tree J_s for subcanopy trees (Dalsgaard 2007b, Dalsgaard in prep.). Thus, in MAN, the weighted J_s was scaled by the fraction of stand basal area per hectare active in the transport of water (77%). In NAT, scaling accounted for differences in canopy positions among sample trees and the resulting weighted J_s was related to the basal area within the crown projection area of the sample trees. From the measurements of eight crown radii for each tree the crown projections were calculated from 8 x 1/8 ellipse (Brunner 1998). The plot crown projection area

adjusted for overlap was 618 m^2. Within this area all trees were either i) dominant or co-dominant, ii) suppressed subcanopy trees or iii) released subcanopy trees. Weights for each group i)-iii) were calculated from the estimated amount of conducting xylem area multiplied by the fraction of the tree crown present within the plot area. The resulting weights were i) 71%, ii) 14% and iii) 16%. For comparison, the relative weights of the three groups among the sample trees only were 80%, 10% and 11%. In NAT, European beech occupied 74% of the basal area within the plot crown projection area. European beech E is referred to as E_{day} (daily sum) or E_{diu} (diurnal values) using a subscript of NAT or MAN when necessary to refer to a specific site. E is the entire canopy transpiration in MAN. E is the fraction of total canopy transpiration in NAT originating from European beech. Sap flow of European beech has been found to exceed that of several co-occurring species (Hölscher et al. 2005), thus E presumably comprises the majority of total plot transpiration.

Canopy conductance

Canopy conductance (g_c, $m \cdot s^{-1}$) was calculated using the Penman-Monteith equation as in Magnani et al. (1998):

Eq. (1)
$$\lambda E = \frac{sR_n + \rho_a c_p D_r g_a}{s + \gamma\left(1 + \frac{g_a}{g_c}\right)}$$

where E is the canopy transpiration per unit ground area ($kg \cdot m^{-2} \cdot s^{-1}$), λ is the latent heat of vaporization of water (≈2.45 x 10^6 $J \cdot kg^{-1}$), s is the slope of the saturation vapour pressure-temperature curve ($Pa \cdot K^{-1}$), R_n is net radiation ($W \cdot m^{-2}$), ρ_a is the density of dry air (≈1.204 $kg \cdot m^{-3}$), c_p is the specific heat capacity of air (1012 $J \cdot kg^{-1} \cdot K^{-1}$), D_r is the vapour pressure deficit at reference height (Pa), g_a is the canopy aerodynamic conductance to scalars ($m \cdot s^{-1}$) and γ is the psychrometer constant (≈66.1 $Pa \cdot K^{-1}$). R_n was estimated from R_g (Federer 1968 in Rosenberg et al. 1983). The aerodynamic conductance g_a ($m \cdot s^{-1}$) was calculated from wind speed measurements as in Granier et al. (2000a):

Eq. (2) $$g_a = \frac{k^2 u}{\ln[(z-d)/z_0]}$$

where k is Von Kármán's constant (0.41), u is wind speed at a reference height (m $\cdot$ s^{-1}), z is the reference height (m), d is the zero plane displacement (m) and z_0 is the surface roughness (m). In NAT, open-field u was extrapolated from 2 m to 57 m height using the logarithmic wind profile (Monteith and Unsworth 1990): u = (u_* / k) ln [(z – d) / z_0], where u_* is the friction velocity (m $\cdot$ s^{-1}). Observations with D < 2 hPa, observations during and 2 hours after rain and measurements during early morning and night hours were not included. Further, to isolate data with non-limiting SWC and avoid errors due to low D, the sensitivity of model fit (r^2 -value, PROC NLIN, SAS 8.2, SAS Institute, Cary, NC) to thresholds of SWC_{REL} (0-0.7) and D (2-6 hPa) was investigated for the Lohammer model for g_c (Lindroth 1993, Granier et al. 2000a). Data subsets giving a high r^2 -value were assumed to represent the best selections for further analyses. The adjusted r^2 -values ranged from 0.10 to 0.71 in NAT and from 0.07-0.44 in MAN. Selected thresholds were 0.5 (SWC_{REL}) and 6 hPa (D). In NAT, using stand D consistently resulted in slightly higher r^2 -values than open-field D and therefore stand D was used in all analyses. For daily data only the SWC_{REL} threshold is relevant.

Tree mean leaf level conductance

A mean leaf level total conductance (mm $\cdot$ s^{-1}) for individual trees in NAT was calculated as in Köstner et al. (1992):

Eq. (3) $$g_{Ltree} = k \cdot \frac{E_L}{D}$$

E_L is individual tree transpiration (mm $\cdot$ $hour^{-1}$) per leaf area (LA) and D is the air vapour pressure deficit (kPa). k is unit conversion factor; k = $\rho \cdot G_v \cdot T_a$ = 36.91 kPa at 15ºC and when g_{Ltree} is expressed in mm $\cdot$ s^{-1}. ρ is the density of water (998 kg $\cdot$ m^{-3}), G_v is the gas constant (0.462 $m^3 \cdot kPa \cdot kg^{-1} \cdot K^{-1}$) and T_a is the air temperature (K). g_{Ltree} was calculated from J_s for June, July and August. The selection of data was as described for g_c, only the threshold for SWC_{REL} was

higher (0.6). LA for individual trees was estimated from measurements of crown geometry (for each tree: 8 crown radii, tree height and height of crown base) using a 3D crown representation with a spatial resolution of 0.2 m (Brunner 1998). LA for the 12 sample trees agreed well with leaf area predicted from a regression based on the destructive sampling of seven trees (LA_{reg}; Schmitt 1997, in: Schäfer et al. 2000), $LA = 1.099 \cdot LA_{reg}$ (r^2 -value 0.83). The parameters in the crown representation model including leaf area density and crown shape were calibrated for the site (Brunner unpubl.). The values of these parameters influences LA, however, for the purpose of this study the ranking of the trees and not the absolute values for g_{Ltree} are important.

Statistical analyses

To test for a linear relationship in E between the two sites, the first analysis compared E_{day} and E_{diu} in the two stands by testing the significance ($p < 0.05$) of a quadratic term (α_2) in the regression model: $E_{NAT}=\alpha_1 \cdot E_{MAN} + \alpha_2 \cdot E_{MAN}^2$. For E_{diu}, observations (all or those with PPFD > 1000 µmol $\cdot$ $m^{-2} \cdot s^{-1}$) were from 14 days in June and July with P=0 during the day and with high soil water content (SWC_{REL} > 0.5) or from four of these days with the highest D_{max} (12-20 hPa). Further, the slope in the regression: $E_{diu\text{-}NAT}$ = intercept + slope $\cdot$ $E_{diu\text{-}MAN}$ was related to D_{max} to examine the day-to-day variation in the relationship between $E_{diu\text{-}NAT}$ and $E_{diu\text{-}MAN}$. In a second analysis the diurnal course of the standardized E_{diu} ($E_{diu\text{-}standard}$) was compared for the sites in the same 14 or four days as above. Standardized values were calculated from mean E_{diu} by subtracting the mean and dividing by the standard deviation (Weisberg 1985). A sine curve was fitted to these data ($E_{diu\text{-}standard} = a \cdot \sin(time/c + b)$, where a, b and c are fitted parameters) and the significance of site-specific parameters was tested (F-test, $p < 0.05$). It was assumed that any correlations among observations due to time were accounted for by using a sine curve. In a third analysis, the sensitivity of g_c to D and the relationship between g_{Ltree} and tree height was investigated by using high-light observations (PPFD > 1000 µmol $\cdot$ $m^{-2} \cdot s^{-1}$) to estimate the model:

Eq. (4) $g = g_{ref} - m \cdot \ln D$ (Oren et al. 1999, Schäfer et al. 2000).

where g_{ref} is a reference conductance (at D=1 kPa) and m is the sensitivity to D, both are fitted parameters. At the canopy level, g and g_{ref} are denoted g_c and g_{cref} and at the tree level they are denoted g_{Ltree} and $g_{Ltree\text{-}ref}$. An F-test ($p < 0.05$) was used to test differences in m on the canopy level (g_c). g_c was standardized to eliminate differences between sites due to leaf area. For individual trees, $g_{Ltree\text{-}ref}$ was regressed on tree height. Models were fitted to data selected according to thresholds in SWC_{REL} and D identified earlier. To ensure that the models represent the upper boundary, observations above the mean + standard error in 2 hPa intervals of D were used. Observations with D >18 hPa were combined. This procedure is from Schäfer et al. (2000) only i) all data falling above the mean + standard error was used (without averaging) and ii) standard error, not standard deviation as this would have eliminated large parts of the data set especially for NAT at high and intermediate D. Final conclusions were insensitive to this choice. Analyses were made using SAS Version 8.2 (PROC NLIN, GLM, CORR; SAS Institute, Cary, NC).

Results and discussion

Meteorological conditions

The period with simultaneous measurements was characterized by mild weather and meteorological conditions were similar for the two sites. Correlation coefficients for daily mean T_a, D_{mean}, D_{max} and R_g were between 0.95 and 0.99. Correlation coefficients for daily mean u, daily SWC_{REL} and P were 0.90, 0.79 and 0.62 respectively. Minimum SWC was 11.2% in NAT reached on September 1, and 11.3% in MAN reached on August 30. In the period with simultaneous measurements the highest observed D_{max} was 21.6 hPa in MAN, and 22.3 hPa in NAT and in this period mean T_a was 14.5 °C in NAT and 14.2 °C in MAN. D_{max} exceeded 15 hPa for only three days (June 19-21).

Daily transpiration

Observations of E_{day} were higher in MAN than in NAT. The highest values were observed in mid June. During the period with simultaneous measurements the highest observed E_{day} was reached on June 20 for both sites. It was 2.6 (0.47) mm for NAT with a SWC of 19% (standard error of the mean in parenthesis). For MAN it was 3.1 (0.19) mm at a SWC of 20%. Before the period with

simultaneous measurements a higher E_{day} of 3.5 (0.16) mm at a SWC of 25% was observed for MAN on June 10. This observation qualified as an outlier, but nothing indicated technical errors. Though European beech basal area were similar at the sites (see Table 1), $E_{day\text{-}NAT}$ was generally 80% of $E_{day\text{-}MAN}$. Presumably, the LAI originating from European beech was lower in NAT than in MAN, resulting in a lower plot transpiration rate, however, the species specific LAI was not measured in NAT. E_{day} was comparable to measured European beech transpiration in other studies: We found the maximum daily E to be 0.8 mm $\cdot$ m^{-2} leaf area in MAN and in the range 0.6-0.8 in NAT depending on an assumed fraction of European beech LAI on the plot (75-100% of stand LAI). The maximum daily transpiration has been found to be a relatively conservative value of 0.6-0.7 mm $\cdot$ m^{-2} leaf area among measurement years and across stand age (Granier et al. 2000a, Köstner 2001). Total E was 114 mm in NAT measured June 15-September 30, 80% of E in MAN (143 mm) during the same period. Total E in MAN was 203 mm measured May 5-September 30.

Observed E_{day} was controlled primarily by D through a second order polynomial relationship (Figure 1a) and R_g through a linear relationship (Figure 1b). These close relationships indicate that low soil water content was not a major limitation to transpiration. However, low soil water content in late summer probably contributes to the variation in E_{day} at low D_{mean} as the highest observations of D_{mean} were in early summer where soil water content was high. $E_{day\text{-}NAT}$ was closely and linearly related to $E_{day\text{-}MAN}$ for all days as well as for days with high soil water content at both sites (Figure 1c). A quadratic term was not significant in either case ($p>0.05$).

Diurnal transpiration

$E_{diu\text{-}NAT}$ and $E_{diu\text{-}MAN}$ were closely related for the selected days in June and July (Figure 2). A quadratic term was significant ($p<0.0001$) for i) all 14 days and for ii) four of these days with high D_{max}. When the analysis was limited to observations with high PPFD the curvature was not significant in either case, thus the non-linear relationship can be explained by differences in canopy light interception. Subcanopy trees in NAT are shaded by the dominant canopy resulting in a delay in transpiration relative to MAN as was also observed by Martin et al. (1997).

For a regression of $E_{diu\text{-}NAT}$ on $E_{diu\text{-}MAN}$ ($E_{diu\text{-}NAT}$ =intercept + slope · $E_{diu\text{-}MAN}$) it was observed that the slope was higher for four days with high D_{max} than for all 14 days. Using the above regression for each of the selected days (observations with high PPFD) revealed that the slope increased significantly with D_{max} (r^2 -value 0.73, p=0.03), but only when using the six days with n>6 observations (insert Figure 2). This result did not depend on the origin of measured D_{max} (climate stations in NAT or MAN). For each of these days there was a strong relationship between $E_{diu\text{-}NAT}$ and $E_{diu\text{-}MAN}$ with r^2 -values between 0.64 and 0.99. Thus, generally $E_{diu\text{-}NAT}$ was lower than $E_{diu\text{-}MAN}$ but the relationship approached unity for high rates of transpiration and on days with a high evaporative demand. This result indicates that the European beech canopy in MAN may experience a more pronounced stomatal closure due to high D (Meinzer et al. 1997, Hogg and Hurdle 1997) than in NAT, resulting in a stabilization of transpiration for the canopy as a whole or a more severe limitation in hydraulic conductance in the root-shoot pathway. In this study we cannot locate such limitations to specific segments in the soil-plant-atmosphere-continuum. The result is based on a limited amount of data.

From the mean diurnal curves in Figure 3, it was observed that transpiration in NAT had a more distinct mid-day peak than in MAN. $E_{diu\text{-}standard}$ was higher in NAT than in MAN around noon, but the parameters in the sine curve were not significantly different between sites (14 days r^2 -value 0.98, four days r^2 -value 0.97). $E_{diu\text{-}NAT}$ tends to decrease faster in the afternoon than $E_{diu\text{-}MAN}$. This could be an additional reason why E_{day} is lower in NAT than in MAN. The mean values for PPFD and D for the two sites for the 14 selected days were highly correlated with correlation coefficients of 0.98 for PPFD and 0.96 for D. For the individual observations correlation coefficients were 0.87 for D and 0.92 for PPFD.

Calculated correlation coefficients revealed that the mean $E_{diu\text{-}NAT}$ for the 14 selected days was closer correlated with PPFD (0.91) than with D (0.84), whereas $E_{diu\text{-}MAN}$ was closer correlated with D (0.96) than with PPFD (0.80). For the individual observations of E_{diu}, correlations with D and PPFD within each site were ranked in a similar manner. The higher correlation to D in MAN could be due, at least partly, to the positions of the D measurements relative to the canopy surface. A high atmospheric decoupling of transpiration (Jarvis and McNaughton 1986) is indicated where transpiration is related relatively more to radiation than to D (Wullschleger et al. 2000). Transpiration of European beech has been found

to be highly coupled to the atmosphere with values of decoupling ranging from 0.05 to 0.28 (Herbst 1995, Magnani et al. 1998, Granier et al. 2000a) indicating that stomatal closure is the main control of transpiration. At our two sites, differences in the correlation with D between canopies may also be caused by the canopy structure, especially the presence of subcanopy trees in NAT. In NAT, the computed correlation coefficients between individual tree transpiration and D at non-limiting soil water content were higher for canopy trees (0.72-0.86) than for subcanopy trees (0.67-0.72, tree height < 20 m). Turbulence in the canopy space affects transpiration of emergent and dominant trees more than that for trees lower in the canopy (Hollinger et al. 1994, Köstner et al. 1992) and a higher decoupling for saplings in the understorey than for canopy trees of Acer rubrum L. was reported in Wullschleger et al. (1998, 2000). We suggest that European beech transpiration in NAT is slightly more decoupled from the atmosphere than in MAN.

In this study, a lag-phase between sap flow and D was not found as was also the case for European beech in other studies (Granier et al. 2000a). Sap flow does persist late in the evening (see Figure 3), thus some refilling of vessels occurs. In this study, we concentrate on day-time observations where sap flow is high and the influence of the refilling of vessels is expected to be small. The importance of a lag-phase is related to severe soil water depletion (Phillips and Oren 1998), which was not observed at our sites.

Canopy conductance

Calculated g_c was slightly higher in MAN than in NAT (Figure 4a-b). At D=10 hPa g_c reached approximately 0.01 $m \cdot s^{-1}$ in MAN which is similar to g_c calculated in earlier years at the same site from micrometeorological measurements (Dellwik 2003). In NAT g_c reached approximately 0.008 $m \cdot s^{-1}$ (at 10 hPa). Estimates of g_c from the present study were slightly lower than those shown for three European beech sites (Germany and France; Granier et al. 2000a, Granier et al. 2003) with g_c (at 10 hPa) of approximately 0.010-0.013 $m \cdot s^{-1}$ and higher than values found for European beech in Italy of 0.006 $m \cdot s^{-1}$ (Magnani et al. 1998), and in Steigerwald (0.005 $m \cdot s^{-1}$), Germany (Granier et al. 2003). Higher LAI at the French sites may explain that these estimates were higher than those observed here (Granier et al. 2000b).

In Figure 4a-b, an upper boundary for g_c is indicated after the application of the selection criteria based on SWC_{REL} and PPFD. Figure 4c shows a higher boundary-line g_c (Eq. (4)) in MAN than in NAT, but otherwise the curves appear quite similar for the two sites. For standardized values (Figure 4d), the slope relative to D seems steeper in NAT than in MAN. The standardized curves were significantly different (F-value 6.6; $p<0.005$), but not the parameter m which represents the sensitivity to D ($g_{c\text{-}ref}$ from the standardized boundary-line g_c differed between sites: MAN>NAT). Thus, the sensitivity of European beech g_c to D does not seem to depend on canopy structure and height distribution like those represented at our study sites. Preliminary analyses showed that this result was insensitive to the choice of D (field or forest) and to a criterion in the boundary-line selection method (standard error or standard deviation; see section Statistical analyses). The predicted curves for the g_c boundary-lines may change when using other criteria for the selection of boundary-line data. However, the selected observations do represent light saturated data with low errors in D measurements as well as non-limiting soil water conditions. Thresholds applied in this study to avoid errors in D as well as to ensure non-limiting soil water conditions were similar to those used by other authors (Ewers and Oren 2000, Granier et al. 2000a, Dellwik 2003). For a warmer summer, boundary-line g_c would be based on a more balanced data set. Our result agrees with other studies where transpiration for European beech was compared among sites and across age, height and density (Granier et al. 2000a, b, Köstner 2001, Granier et al. 2003). The largest sample tree in NAT was smaller than the largest and presumably older trees in this forest with stem diameter up to approximately 1.4 m. Including sap flow of these trees in a stand transpiration estimate may have changed this result. Reduced transpiration with age (Delzon and Loustau 2005) and in trees of low vitality (Vincke et al. 2005) has been reported.

In NAT the wind speed used in the calculation of g_c was predicted using a logarithmic profile. This may introduce errors in the calculation of g_a and the gradient in wind speed (tower measurements at 37 and 57 m) was steeper for the measured values in MAN than for the predicted values in NAT. When extrapolating u to 57 m, calculated g_a was 5-37% larger than in MAN. Extrapolating to 37 m resulted in g_a values nearly twice as high as in MAN. Though higher wind speeds and a different canopy structure could warrant higher g_a values in NAT, it seems that extrapolating u to 57 m introduces the smallest errors of the two alternatives.

Because information on tree crown projection (as in NAT) was not available in MAN, E was estimated based on stand basal area. It is likely that, if crown projection had been used for the prediction of E in MAN, the estimate would have been slightly different (with a constant fraction) than the present estimate. Analyses in this study are based on relative or on standardized values and the conclusions should not be affected. Estimating E in NAT based on stand basal area was not relevant due to the need to distinguish among several classes of trees.

Individual tree leaf level conductance

Individual tree reference conductance, $g_{Ltree\text{-}ref}$, was generally low for tall trees, but showed a high variability for small tree. For the tree level, parameters in Eq. (4) ($g_{Ltree\text{-}ref}$ and m) are given in Table 2. Predicted g_{Ltree} at 10 hPa ranged from 1.2-4.4 mm $\cdot s^{-1}$ corresponding to approximately 50-183 mmol $\cdot m^{-2} \cdot s^{-1}$. A similar range (50-150 mmol $\cdot m^{-2} \cdot s^{-1}$) was found by Schäfer et al. (2000) which indicates that though tree leaf area in the present study was not directly measured but estimated from crown geometry it may give a fair representation of true tree leaf area. A general dependency of $g_{Ltree\text{-}ref}$ on tree height as hypothesized does not emerge (Figure 5) and this was in contrast to the results in Schäfer et al. (2000). Other studies have found that stomatal conductance does not vary systematically with height (Phillips et al. 2002). Ryan et al. (2006) states that hydraulic limitation with increasing tree height is common but not universal and that effects of gravity and a long path length from soil to leaf may be mitigated by a decrease in the leaf area:sapwood area ratio, a reduced minimum leaf water potential or an increase in sapwood conductivity or in stem capacitance.

As found in Oren et al. (1999) $g_{Ltree\text{-}ref}$ is positively related to the sensitivity of leaf level conductance to D (insert, Figure 5). In the present study the results were not sensitive to the boundary-line selection (standard error or standard deviation, see section Statistical analyses).

A canopy opening in NAT added to the complexity of the canopy structure and some of the subcanopy trees were released whereas others were in shaded positions. It was not possible to explain the variation in $g_{Ltree\text{-}ref}$ by the differences in crown exposure among the 12 sample trees and it is possible that crown exposure was not sufficiently well described. For trees below the main canopy,

the variation in $g_{Ltree\text{-}ref}$ may also be a result of an acclimation process to meet the higher levels of light and evaporative demand in this dynamic environment. Lemoine et al. (2002) showed that recently thinned branches of European beech exhibited a higher stomatal conductance and xylem-leaf water potential gradient than both shade-branches and sun-exposed branches.

In this study we used sap flow measurements obtained at non-limiting soil water conditions and these should not be subject to the high variability among sensors and trees found at low soil water content (Čermák et al. 1993, 1995). The transpiration of subcanopy trees may be more sensitive to low soil water content than the canopy as a whole (Dawson 1996, Piutti and Cescatti 1997) which is why the threshold for SWC_{REL} was higher for individual trees than for the entire plot. One sensor for each tree in NAT should therefore be sufficient to show expected patterns among trees as also seen in other studies (Köstner et al. 1992, Čermák et al. 1993, Martin et al.1997, Schäfer et al. 2000).

In NAT, edge effects of meteorological variables cannot be excluded as the site is a narrow strip of forest surrounded by open fields and lake. Wind speed and air humidity have been shown to influence the climate inside forests up to 200 m from the edge depending on aspect and wind direction (Chen et al. 1995). Wind speed below the canopy in NAT was generally below 1 $m \cdot s^{-1}$ and only rarely above 2 $m \cdot s^{-1}$, whereas wind speed from the open field reached above 8 $m \cdot s^{-1}$. Thus, an edge effect of wind was not strong, but cannot be excluded and the regulation of transpiration in NAT may differ from that of European beech stands in a closed forest environment. In this study the stands were characterized as a natural and managed stand to highlight the potential differences in transpiration and canopy conductance among stands differing in management type and height distribution. Stand characteristics other than those in focus here (e.g. below ground structure, age) could have affected the results and further studies are important for a more detailed understanding of the variability in transpiration.

Conclusions

In spite of differences in canopy structure between the two sites – a heterogeneous natural forest and a mature homogenous even-aged stand - results from this study show that the transpiration and boundary-line canopy conductance for European beech were similar during the summer 2000. Further, tree height was not found to

influence individual tree leaf level conductance. Thus, for estimation of European beech transpiration on forest or regional scale there should be no need to consider effects of tree height within the limits observed for this study. Some tendencies emerged from the comparison of diurnal transpiration: For low PPFD, transpiration in NAT increased more slowly than in MAN illustrating the effect of shading from the main canopy on the transpiration from subcanopy trees. Transpiration in NAT was closer correlated to PPFD than to D whereas the opposite was observed in MAN. In NAT, transpiration for canopy trees was closer correlated to D than for trees below the main canopy and we suggest that European beech transpiration in NAT is slightly more decoupled from the atmosphere than in MAN. Though diurnal transpiration was generally lower in NAT than in MAN, the relationship approached unity for high evaporative demand and MAN may experience limitations in the hydraulic pathway at high transpiration to a larger extend than NAT. The climate of the 2000 growing season was mild. Different results and significant differences between stands could emerge for periods with a higher evaporative demand.

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Tables

Table 1. Stand structure parameters at two European beech dominated sites in eastern Denmark.

	NAT[c] (Suserup)	MAN[a] (Soroe)
Basal area ($m^2 \cdot ha^{-1}$)	40.2 Sap flow plot: 39 of which 29 is Fagus sylvatica L.	29
Stand density (trees $\cdot ha^{-1}$)	733	283
Mean tree height (m)	13.3	25±1
Stand top height (m)	28.4	-
Mean tree diameter (cm)	18	38
Leaf area index ($m^2 \cdot m^{-2}$)	4.6[b] (August)	4.2[b] (August-September)
Tree species	Fagus sylvatica L. Fraxinus excelsior L. Quercus robur L. Ulmus glabra Huds.	Fagus sylvatica L.

[a] Stand data from: Pilegaard et al. (2003) and Mikkelsen (unpubl.). Height is the observed canopy height from the tower (Mikkelsen pers. obs.).

[b] Measured with the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA).

[c] For the description of stand structure all trees above 45 mm stem diameter in a 6400 m^2 area around the sap flow plot were measured. Top height is the mean height of the 100 tallest trees ha^{-1}.

Table 2. Sap flow sample trees in Suserup Forest, eastern Denmark, for the summer 2000. Height, stem diameter (at 1.3 m height) and estimated leaf area (LA) are given for each tree. Trees, where the radial variation of sap flow was measured in 2001 are marked with * (Dalsgaard 2007b). Parameters for the model: $g_{Ltree} = g_{Ltree\text{-}ref} - m \cdot \ln D$ fitted to boundary-line observations for each sample tree in NAT at high soil moisture are shown. See Eq. (4). The 95% confidence intervals are given for the fitted parameters $g_{Ltree\text{-}ref}$ and m. g_{Ltree} is the calculated leaf level conductance and D is the air vapour pressure deficit.

Tree #	Height (m)	Diameter (cm)	LA (m^2)	adj. r^2 -value	m ($mm \cdot s^{-1} \cdot hPa^{-1}$)	$g_{Ltree\text{-}ref}$ ($mm \cdot s^{-1}$)
7	16.0	19.0	42.5	0.65	2.2464 ± 0.528	3.3221 ± 0.161
8	18.9	21.0	94.8	0.69	0.9550 ± 0.372	1.7660 ± 0.061
10	15.4	11.0	35.8	0.50	0.9755 ± 0.130	1.4206 ± 0.098
11	19.8	22.0	139.7	0.83	1.1793 ± 0.155	1.7142 ± 0.048
12*	25.5	37.0	310.1	0.84	0.8366 ± 0.120	1.3089 ± 0.040
13	29.0	69.7	422.5	0.72	0.5102 ± 0.101	1.3677 ± 0.032
14	27.6	49.5	298.1	0.87	1.4958 ± 0.176	1.6651 ± 0.055
15	14.2	10.5	21.4	0.48	1.5970 ± 0.535	2.3431 ± 0.155
17*	26.8	35.0	278.6	0.79	0.6100 ± 0.097	1.0838 ± 0.030
18	18.1	17.0	30.8	0.71	2.9117 ± 0.561	4.2268 ± 0.170
19*	25.5	36.5	161.7	0.80	1.2705 ± 0.211	2.4338 ± 0.068
20*	24.9	42.0	280.1	0.88	1.4400 ± 0.156	1.9801 ± 0.050

Figures

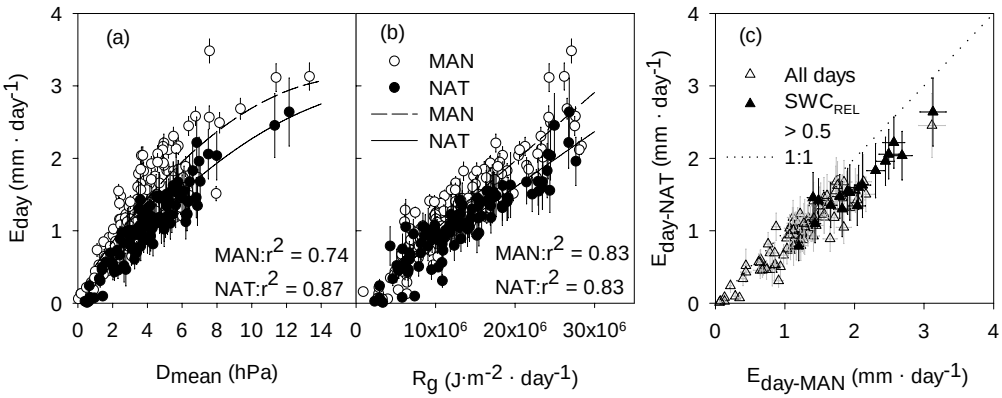

Figure 1. Daily European beech transpiration (E_{day}, mm · day^{-1}) relative to daily values of (a) vapour pressure deficit (D_{mean}) including a polynomial model ($p<0.0001$) and (b) global radiation (R_g) including a linear model ($p<0.0001$). Observations were from 108 days in NAT (Suserup) and 124 days in MAN (Soroe), eastern Denmark. (c) shows $E_{day\text{-}NAT}$ vs. $E_{day\text{-}MAN}$. A linear model yielded an r^2 -value of 0.91 for all 108 days and 0.88 for18 days with high soil water content at both sites. Error bars show ± one standard error of the mean. SWC_{REL} is the relative soil water content (see text).

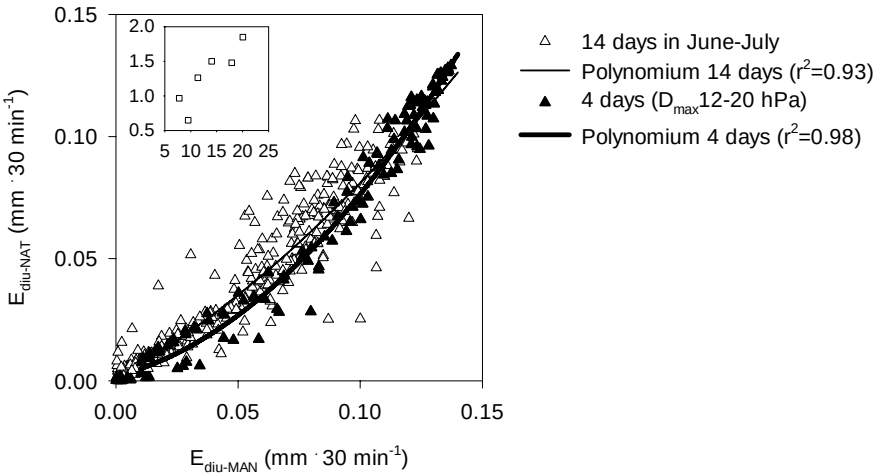

Figure 2. Diurnal transpiration in NAT vs. MAN ($E_{diu-NAT}$ vs. $E_{diu-MAN}$) for European beech at two sites in eastern Denmark. Observations are from 14 days in June-July (n=497) and from four days with high D_{max} (n=137). Curves represent second order polynomia. Soil water content was high for all observations (SWC_{REL} > 0.5). Insert: Estimated slope for each day ($E_{diu-NAT}$ = intercept + slope · $E_{diu-MAN}$) relative to D_{max} (x-axis) for days with n > 6.

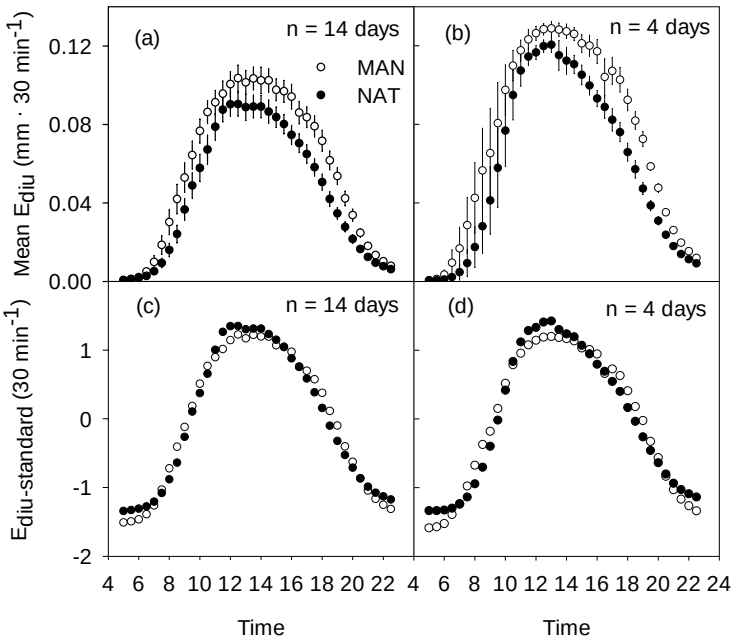

Figure 3. Daily course of transpiration in NAT (Suserup) and MAN (Soroe), eastern Denmark. Upper panels show the mean canopy transpiration (mean E_{diu}) for (a) 14 days in June-July and (b) four days with high D_{max} (12-20 hPa). Lower panels show the standardized canopy transpiration ($E_{diu\text{-}standard}$) for (c) 14 days in June-July and (d) four days with high D_{max}. Error bars show ± one standard error of the mean. Observations in (c) and (d) are standardized using the mean and standard deviation. Soil water content was high for all observations (SWC_{REL} > 0.5).

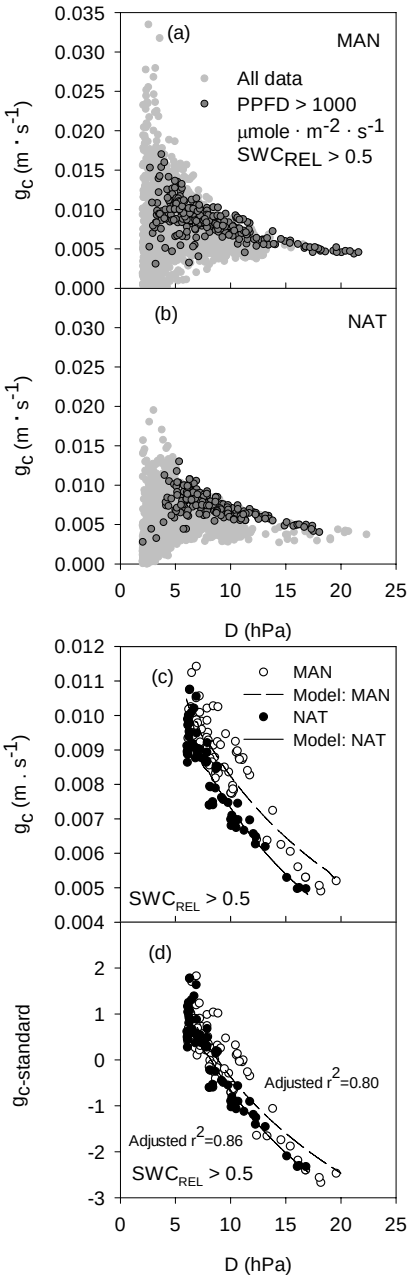
(a)
MAN
All data
PPFD > 1000
μmole · m-2 · s-1
SWCREL > 0.5
gc (m · s-1)
(b)
NAT
D (hPa)
(c)
MAN
Model: MAN
NAT
Model: NAT
SWCREL > 0.5
gc (m . s-1)
(d)
Adjusted r2=0.80
Adjusted r2=0.86
SWCREL > 0.5
gc-standard
D (hPa)

Figure 4. European beech canopy conductance (g_c) calculated from sap flow measurements in 2000: (a) in NAT (Suserup) and (b) in MAN (Soroe), eastern Denmark. PPFD is the photosynthetic photon flux density, SWC_{REL} is the relative soil water content (see text) and D is the air vapour pressure deficit. Boundary-line observations of g_c for the two sites are shown in (c) and standardized boundary-line observations ($g_{c\text{-standard}}$) are shown in (d). Observations are standardized using the mean and standard deviation (see text). Model: $g_c = g_{cref} - m \cdot \ln D$, see Eq. (4).

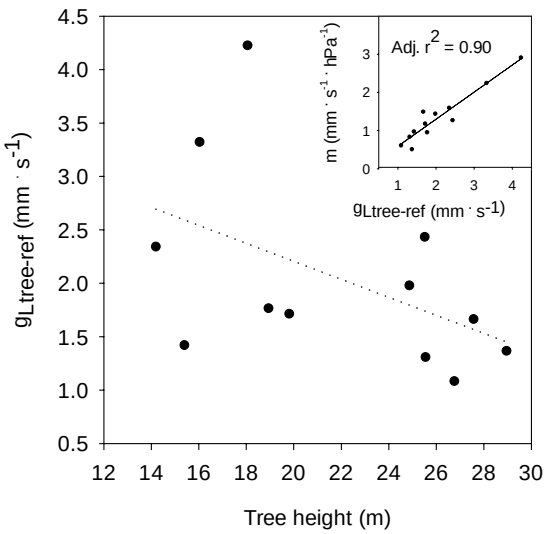

Figure 5. $g_{Ltree\text{-}ref}$ relative to tree height for 12 European beech trees in NAT (Suserup) in eastern Denmark. Regression is not significant (p=0.11). Insert: m (the sensitivity of g_{Ltree} to changes in D) relative to $g_{Ltree\text{-}ref}$, m and $g_{Ltree\text{-}ref}$ are fitted parameters in the model $g_{Ltree} = g_{Ltree\text{-}ref} - m \cdot \ln D$, where D is the air vapour pressure deficit and g_{Ltree} is the individual tree leaf level conductance calculated from sap flow measurements.

Paper V

Water budgets in a natural and a managed temperate deciduous forest - contrasting small canopy gaps and the surrounding closed forest

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Abstract

Small scale disturbances like tree mortality or group harvesting affect soil water- and nutrient dynamics. Few studies have calculated water balance components in small canopy gaps. Using the one-dimensional process-based CoupModel, we simulated the water budget in canopy gaps, gap edges and closed forest in a natural mixed forest reserve (Fagus sylvatica L., Fraxinus excelsior L., Quercus robur L.) and a managed monospecific mature stand (Fagus sylvatica L.). The model was calibrated using measured soil water content as well as throughfall and stemflow volumes. It was applied in a daily time resolution and the meteorological condition in the gaps, characterized by low incident radiation, was specifically considered. Simulated annual drainage was 76-104% higher in canopy gaps than in the closed forest (497-644 vs. 282-319 mm). In gap edges the simulated annual drainage was 7-8% higher in the natural forest and 35% higher in the managed forest relative to the closed forest conditions. The calibration of the model was best defined for closed forest conditions. Application for the edge and gap positions were useful to identify the possible horizontal processes in the water cycle near a gap, but estimates in the water budget may be influenced by the inability of the model to represent these processes. The model could not reproduce a moderate decline in gap soil water content in mid and late summer periods and it is suggested that this decline is caused by soil water extraction by trees in the edge and closed forest. The simulated gap soil water content was insensitive to the parameterization of leaf area index of the gap vegetation. In the closed forest, simulations for the natural mixed forest displayed a higher interception loss and a lower transpiration relative to the stand leaf area than the simulations for the managed monospecific stand. Further, the calibrated value of the maximum stomatal conductance was lower in the natural than the managed stand. Simulated annual soil evaporation in the closed forest was 28-31% of total evapotranspiration. These values are high and further research should include the collection of data to describe soil and forest floor evaporation.

Keywords: Evaporation; Forest management; Gap; Mixed forest; Natural forest; Stand structure; Water balance

Introduction

Canopy gaps are formed after wind-throw or tree mortality in natural forests or created by forest management following single-tree or group harvesting. The soil moisture dynamics have been shown to differ in closed forest and in canopy gaps (Bauhus and Bartsch, 1995; Aussenac, 2000; Gray et al., 2002; Ritter et al., 2005a) leading to differences also in the soil water budgets (Ritter et al., 2005b; Ritter and Vesterdal, 2006). For economic reasons as well as to increase biodiversity and enhance ecological sustainability, uneven-aged stand structures are promoted in many forest areas. Changes from homogenous even-aged rotation forestry to stands characterized by group or single tree harvesting may affect the forest water budget (Zirlewagen and von Wilpert, 2001) thus also the amount and timing of water available for surface water and groundwater recharge. Predicted drainage is used to estimate fluxes of nutrients from forest ecosystems (Christiansen et al., 2006) and in heterogeneous forests both nutrient- and water budgets may depend on canopy density and disturbance history (Bauhus et al., 2004; Ritter et al., 2005b; Ritter and Vesterdal, 2006; Ritter and Bjørnlund, 2005). However, while the microclimate and soil water dynamics in small canopy gaps are relatively well documented (Gray et al., 2002; Ritter et al., 2005a), only few studies include the prediction of drainage and evaporation fluxes and, if so, mostly in a monthly time resolution (Ritter et al., 2005b; Vilhar et al., 2005; Ritter and Vesterdal, 2006). A higher temporal resolution would increase the accuracy of the predictions of drainage fluxes, and using meteorological input reflecting the microclimate in a canopy gap would improve our understanding of the changes in forest functionality achieved through manipulation of the stand structure. Studies in natural deciduous forests in northern Europe are rare since only few natural forests remain. However, these forests act as models for forest management in terms of stand structure (Hahn et al., 2007). The function of natural forests is therefore highly relevant. Differences in the soil water dynamics are due to a range of processes. In canopy gaps, a lower interception loss (Zirlewagen and von Wilpert, 2001; Dalsgaard, 2007a) and a lower plant water uptake and root density (Brockway and Outcalt, 1998; Ammer and Wagner, 2002; Müller and Wagner, 2003; Dalsgaard, 2007a) contribute to high soil moisture. In xeric forests (Heinemann et al., 2000; Vilhar et al., 2005) and in forests with dense forest floor vegetation (McGuire et al., 2001) soil moisture effects may be small. Water use of trees at the edge of the canopy gap may be higher than of trees in the surrounding closed forest (Cienciala et al., 2002; Dalsgaard, 2007b; Dalsgaard, in prep.). Thus,

although higher soil moisture in canopy gaps is expected, some processes work to mitigate this and the prediction of the drainage flux and evapotranspiration is not straightforward.

In this study the CoupModel (Jansson and Karlberg, 2004) is applied in a daily time resolution to simulate the water budget in canopy gaps, the edges of these gaps and in the surrounding closed forest in two deciduous forests in eastern Denmark: a conventionally managed even-aged mature stand of European beech (Fagus sylvatica L.) and a near-by European beech dominated natural forest reserve. Objectives are i) to apply the model in a complex stand structure and, ii) to compare the water budget in the two forests in closed forest conditions. We hypothesize that the drainage flux is highest in a small canopy gap (2/3-1/1 of stand height), in-between at the edge and lowest in the surrounding closed forest and that the simulated canopy transpiration and interception losses are similar in the two stands due to the dominance of European beech. Results from this study are complementary to recent studies in a number of Danish broadleaved forests including the sites used here (Ritter et al., 2005a; Ritter et al., 2005b; Ritter and Vesterdal, 2006).

Materials and methods

Study sites

The study was performed on two sites in the central part of Zealand, Denmark. Suserup Forest (NAT) is a 19.2 ha mixed deciduous forest (55°22´N, 11°34´E). The unmanaged forest reserve lies on the northern shore of Tystrup Lake and is otherwise surrounded by agricultural fields. An irregularly shaped canopy gap was created in a hurricane in December 1999. Human impact is low and the structure is close to a natural state (Emborg et al., 2000; Hannon et al., 2000; Heilmann-Clausen et al., 2007) with many European beech trees near 300 years of age. Ravnsholte Forest (MAN) is a conventionally managed even-aged 75-year old stand (55º31'N, 11º54'E). A canopy gap was created after felling in January 2001. As a result of management history, stand structure differed between the sites (Table 1, Figure 1). The 30 year mean annual air temperature is 8.1°C and the mean annual precipitation is 644 mm (NAT) and 635 mm (MAN) (Frich et al., 1997; Laursen et al., 1999). Soils are well drained loamy till developed from moraine deposits (Ritter et al., 2005b; Ritter and Vesterdal, 2006).

Climate data

Standard weather data including air temperature, relative air humidity, windspeed, precipitation and photosynthetically active radiation were obtained 2 m above the ground on a nearby open field (NAT) or newly planted forest area (MAN) approximately 300 m from each of the two sites. Precipitation was corrected for wetting (Vejen et al., 2000) and global radiation was calculated from photosynthetically active radiation (Monteith and Unsworth, 1990; Lambers et al., 1998). Measurements continued through the period June 15, 2000 - September 1, 2001 (NAT) and from June 12 - October 9, 2001 (MAN). On-site data were complemented, primarily in winter and spring periods, by using data from a nearby tower (55º29'13''N, 11º38'45''E) above a mature European beech forest (Pilegaard et al., 2003) or, in a few cases, by using interpolation or standard meteorological observations (Frich et al., 1997; Laursen et al., 1999). Measured open-field wind speed was elevated to compare with tower data (Pilegaard et al., 2003; Monteith and Unsworth, 1990). These open-field data were used in the simulations for the closed forest and for the edges of the canopy gap. During the same periods, windspeed, relative air humidity and air temperature were measured on both sites in the stand (below the canopy near the canopy gap) at 2 m height. In periods without measurements in the stands, regressions for each season between on-site and tower data were used for prediction. In the gaps, precipitation and global radiation was estimated based on on-site measurements (Ritter et al., 2005a; Dalsgaard, 2007a) and studies of gap microclimate (Roussel, 1972; Geiger et al., 1995; Madsen and Larsen, 1997; Aussenac, 2000). Precipitation in the gaps was 76-100% of open-field precipitation. Radiation in the gaps was 14-20% of open-field radiation in summer months and 75% in winter months. These data were used in the simulations for the canopy gaps.

Calibration data

The CoupModel was calibrated using measured stemflow in the closed forest (n=3 in MAN, n=8 in NAT) as well as measured throughfall volumes and TDR-measured (Time Domain Reflectometry) soil water content (SWC, mm) (Topp et al., 1980; Thomsen, 1994; Dalsgaard, 2007a; b) from 28 positions at both sites (Figure 1). Closed forest positions were below the canopy and minimum 1.5 m from the stem of trees bordering the canopy gap (n=10 in NAT, n=12 in MAN).

Canopy gap positions were in open conditions and minimum 1.5 m from the stem of trees bordering the gap (n=10 in NAT, n=12 in MAN). The remaining positions were edge (n=8 in NAT, n=4 in MAN). At each position, four TDR-probes were installed integrating over a 0.14, 0.30, 0.50 and 0.90 m vertical soil profile and measurements are referred to as SWC_{14}, SWC_{30}, SWC_{50} and SWC_{90}. To improve the accuracy SWC_{14} was measured with a 0.2 m long probe installed at an angle. Throughfall and SWC measurements covered the coarse-scale structure of the gap, edge and closed forest conditions but were not stratified to describe possible zones of stemflow and drippoint (Ladekarl et al., 2001; Jost et al., 2004). Stemflow is not specifically represented in the CoupModel and for the calibration of the storage capacity of intercepted water in the model the sum of throughfall and stemflow was used.

Model description

The water balance on the two sites was simulated using the process-based CoupModel (Jansson and Karlberg, 2004; Figure 2). This model has been widely used in studies of evaporation and water balance in forests (Eckersten et al., 1995; Persson, 1997; Jansson et al., 1999; Ladekarl et al., 2005; Christiansen et al., 2006). It simulates infiltration to and transpiration, evaporation and drainage from a layered soil in one dimension. The central part of the model is two coupled differential equations for water and heat flow solved with an explicit numerical method. The CoupModel was used in a daily time resolution. Soil evaporation was calculated using an iterative surface energy balance approach (Jansson and Karlberg, 2004). Soil heat flows accounted for both convection- and vapour flows. Soil water flows included convective gas flow. Both snow and soil vapour flows were considered. The hydraulic soil properties used the representation of Brooks and Corey (1964) for the retention curves and the model of Mualem (1976) for the hydraulic conductivity. Matrix conductivity equaled total conductivity. The soil columns were divided into 16 layers: in the upper 0.3 m of the soil the layers were 0.03 – 0.06 m in depth, the remaining layers down to the lower boundary of 2.5 m were 0.1 – 0.6 m in depth. The storage capacity of intercepted water was a function of the leaf area index, LAI (storage = $p_{LAI} \cdot LAI + Base$), where p_{LAI} and Base are parameters. The canopy was represented by a single big leaf and transpiration and evaporation of intercepted water was calculated using the Penman combination equation (Monteith, 1965). The canopy surface resistance

(r_s) was estimated from LAI and leaf conductance (g_l) using the Lohammer equation (Lohammer et al., 1980; Lindroth, 1985; 1993):

$$g_l = \frac{R_g}{R_g + g_{Rg}} \frac{g_{\max}}{1 + \frac{(e_s - e_a)}{g_{vpd}}}.$$

$$r_s = \frac{1}{LAI \cdot g_l}$$

R_g is global radiation, (e_s-e_a) is the air vapour pressure deficit and g_{max}, g_{Rg} and g_{vpd} are parameters. Displacement and roughness were functions of the canopy. Estimates of albedo, canopy height, LAI and rooting depth were given as parameters. Roots were exponentially distributed and plant development was considered as static. The root water uptake was determined by a pressure head response as a fraction of the demand from the atmosphere regulated by water potential and a parameter giving the threshold tension where uptake is reduced. If the potential water uptake from a given soil layer was not realized compensatory uptake from other soil layers was possible. This flexibility among soil layers was governed by a parameter where a maximum value of unity results in full compensation. The CoupModel was run for the entire year 2001 (MAN) and 2000-2001 (NAT) including the preceding November and December to initialize the model.

Model parameterization

The model was parameterized for six situations: closed forest, edge and gap conditions on each of the two study sites. All six parameterizations followed the model scheme as outlined above, but differed in some parameter values. The measured parameters and parameter values from the literature used in the model are listed in Table 2 and Table 3. The seasonal development of LAI for the closed forest follow that observed for a nearby mature European beech stand (Pilegaard et al., 2003) with leaves emerging approximately May 1, maximum reached August 1 and complete defoliation December 1. In NAT, LAI was measured in August and it was assumed to be the annual maximum. In MAN, LAI was

measured in June and the maximum was estimated at 4.4 $m^2 \cdot m^{-2}$ following the seasonal development observed by Pilegaard et al. (2003). Leaves emerge later for common ash (Fraxinus excelsior L.) and pedunculate oak (Quercus robur L.) (occupying 40% of stand basal area in NAT) than for European beech, approximately June 1 (Ladefoged, 1952). This was incorporated into the seasonal development of LAI. LAI for NAT was identical for 2000 and 2001 (K. Hahn and P. Madsen, unpubl. data). LAI in the edges and canopy gaps were changed during the model calibration as both were expected to be dynamic due to root expansion during the simulation period. Initial values in the gap edges were 50% of values in the closed forest conditions. Initial values in gaps were 0.5 $m^2 \cdot m^{-2}$ (May-June) and 1.0 $m^2 \cdot m^{-2}$ (July-November). Roots (< 2 mm) were observed in soil profiles in the closed forest down to 0.9 m soil depth though they were few (2-5 dm^{-2}) or very few (1-2 dm^{-2}) beyond 0.5 m. Roots of European beech and sessile oak (Q. petraea (Matt.) Liebl.) are generally most frequent above 1 m depth (Schmid and Kazda, 2001; Leuschner et al., 2001). We assumed a rooting depth of 0.9 m which facilitated model calibration. On these well-drained sites there is likely to be roots beyond 0.9 m. While deep roots are crucial for tree water supply in dry summer periods, the 2000 and 2001 seasons were not particularly dry and the water uptake from below 0.9 m depth is assumed to be a relatively small fraction of total water uptake.

Soil profile descriptions were performed in the closed forest at both sites (Ritter et al., 2005b; Ritter and Vesterdal, 2006). Soil water retention and bulk density was measured in one soil profile in MAN, about 50 m from the canopy gap and in two soil profiles in NAT, both about 25 m from the canopy gap. Four samples were obtained for each soil horizon and soil profile. In NAT, the mean values for soil water retention and horizon depths were used. Data represented the following soil depths measured from the soil surface (cm): MAN: 3-8, 8-32, 32-50, 50-103, 103-123, and for NAT: 3-25, 25-40, 40-49.5, and 49.5-100. Both sites had a 3 cm deep organic layer. Soil water retention was measured in the laboratory (Schjønning, 1985; Dalsgaard, 2007b) at the following levels of tension (pF = log (cm water column)): 1.0, 1.5, 2.0, 2.5, 3.0, 4.2 (= permanent wilting point). The two profiles in NAT deviated in soil water retention in the deepest soil layer, thus soil heterogeneity was a limitation to model calibration. Porosity was estimated from bulk density using the bulk density and porosity given for a Danish forest soil (Christiansen et al., 2006): porosity (%) = -27.58 $\cdot$ bulk density ($g \cdot cm^{-3}$) + 83.77 (R^2-value 0.50). The range in porosity was 38-57% (MAN) and 43-53% (NAT).

Because of a relatively high soil organic matter content in the forest soil, the regression shown above was preferred to the alternative of using a constant specific mineral density. The soil water retention and in-situ porosity (97%) for the organic layer was found from values in the literature (Vesterdal and Raulund-Rasmussen, 1998; Hajnos et al., 2003).

Calibration and test

The order of calibration was (1) closed forest, (2) edge and (3) gap. As the first step in (1)-(2) the parameters determining the storage capacity of intercepted water were calibrated against the sum of measured throughfall and stemflow in periods of 1-4 weeks duration (maximum observation of throughfall+stemflow was 50-60 mm). To evaluate the absolute agreement between the simulated and observed values, the normalized root mean square error (NRMSE) was calculated as

$$\mathrm{NRMSE} = \frac{\left(\left(\sum (x_s - x_o)^2\right) / n\right)^{0.5}}{\overline{x}_o}$$

where x_s is a simulated and x_o is an observed value (e.g. Schelde et al., 1998). A NRMSE = 0 indicates a 100% fit of the model.

As the second step in (1) the maximum stomatal conductance was calibrated using SWC in the summer 2001 (Table 2) corresponding to the period from leaf emergence to the observed minimum SWC. The calibrated parameter values from closed forest conditions were applied in edge (2) and gap (3) simulations and not further changed. The second step in edge (2) and gap (3) conditions were stepwise changes of LAI while optimizing the NRMSE in a comparison of measured and observed SWC. Edge and gap conditions in NAT were calibrated for both years. Growth of roots and tree crowns at the gap edge is expected to influence the water dynamics of both the edges and the gap (Muth and Bazzaz, 2002; Müller and Wagner, 2003; Dalsgaard, 2007a) thus, a model calibration to the 2001 observations may not have fully represented the processes in 2000. During the calibration the NRMSE was minimized while maintaining a linear relationship

between observed and simulated SWC with a slope close to 1. Rooting depth was 0.9 m for closed forest conditions. In edge and canopy gap rooting depth was varied in the range 0.5-0.9 m and the final value was chosen based on the regression slopes. Preliminary studies showed that the agreement between gravimetrically and TDR-determined SWC was best for SWC_{50} and SWC_{90}. These were used primarily in the calibration.

In NAT the simulated SWC was compared to data not used in the calibration: (A) For closed forest conditions, a comparison was made with measured SWC from the 2000 growing season (June 16 – September 1, 2000). This was not possible for the edge and canopy gap as they were expected to change in structure from 2000 to 2001. (B) Simulated SWC June-April 2000 was compared to measured SWC from 31 measurement positions not included in the calibration data set (Dalsgaard, 2007a). These are found in and near the same canopy gap, but were sampled over a shorter period (June 2000 - April 2001, n=19, 9 and 3 in closed forest, edge and canopy gap). The distance between measurement positions was minimum 5 m.

Results

Interception and soil water dynamics

In NAT, the simulated interception in the closed forest was slightly lower than observed interception (Table 4). In the edge it was close to observations in 2000 and slightly higher than observations in 2001. In MAN, simulated interception loss was close to observed values in the closed forest and slightly higher in the edge. Measured soil water dynamics showed that while the canopy gap remained at relatively high SWC_{90} throughout the growing season at both sites, edge and closed forest positions showed a clear decrease (Figure 3 and 4). At edge positions in NAT, SWC_{90} was intermediate between closed forest and gap, but closer to closed forest SWC_{90} in 2001 than in 2000. In MAN, closed forest and edge positions show almost similar growing season SWC_{90}.

In NAT, observed SWC_{50} and SWC_{90} were well represented by simulations in the closed forest and observations were well represented by simulations in all depths at the edge (Figure 4a). SWC_{14} and SWC_{30} were overestimated in the closed forest and the canopy gap. In MAN, observed SWC_{90} was generally slightly overestimated and in edge conditions an overestimation was seen for all depths

(Figure 4b). For NAT, the lowest calibration NRMSE's were found for SWC_{30} and SWC_{50} (Table 5). For MAN, the calibration NRMSE's were low for the closed forest and the canopy gap while they were rather high for the edge because of a general overestimation. Simulations for all three categories in NAT (see Figure 4a) showed decreasing SWC in the period before leaf emergence. This was also observed for measured SWC, but mostly in SWC_{14}, SWC_{30} and SWC_{50}. The evaporation during this period does not seem to affect the observed SWC_{90} to the same extent as in simulations.

Model calibration was first carried out for the closed forest in NAT. After the appropriate changes for the closed forest in MAN in stand structure, soil characteristics, and canopy storage capacity, it was necessary to increase the parameter determining the maximum stomatal conductance controlling canopy transpiration. The weak SWC dynamics in the canopy gap in NAT (Figure 4a) is well simulated for SWC_{14}, SWC_{30} and SWC_{50} in May 2001. In mid- and late summer 2000 and 2001 there is a tendency that simulated SWC is higher than observed, thus not reflecting the actual water uptake or evaporation. Similarly for the canopy gap in MAN (Figure 4b), observations are rather well predicted for May, but in mid- and late summer simulated SWC tends to be higher than observed SWC_{30} and SWC_{50}. At both sites simulated SWC for the canopy gap was insensitive to changes in LAI and rooting depth (not shown). Using the LAI and rooting depth of the closed forests in a simulation with climate input for gaps yielded no or very small changes in simulated SWC and no improvements in the simulation of low SWC in the canopy gap (same or nearly the same NRMSE as in Table 5 for the canopy gaps). This was also the case when changing the parameters of the Lohammer model governing stomatal conductance. Thus, improvements to the canopy gap simulations were not possible. LAI values at the edge were subject to calibration. Initially they were 50% of closed forest LAI. The final calibrated values for edge LAI in NAT were very low in early and mid summer 2000 until August when they increased to values near those of the closed forest (Table 6). In 2001 they were slightly higher than in 2000 during the early summer. Edge LAI in MAN was higher than initial values from June.

For the closed forest in NAT, the comparison of measured SWC in June 16 – September 1, 2000 with simulated SWC based on the calibration against 2001 data showed that observed SWC_{50} and SWC_{90} was relatively well predicted. NRMSE were 0.29, 0.17, 0.05, and 0.14 for SWC_{14}, SWC_{30}, SWC_{50} and SWC_{90}

respectively. Slopes of a regression of simulated vs. observed SWC_{50} and SWC_{90} were 0.77 (R^2 -value 0.98) and 0.91 (R^2 -value 0.97). For gap, edge and closed forest conditions in NAT simulated SWC was compared to observed SWC from 31 measurement positions not used in the calibration. The NRMSE was generally lowest in summer (June 16 - September 1, 2000) and for the closed forest and the edge they were of the same magnitude as for the calibration (Table 7). For the canopy gap and when including all months, values of NRMSE were higher. The R^2-values were generally high in the closed forest and edge, but low for the canopy gap.

Estimated water budgets

Growing season (May-October) as well as annual water budgets differed markedly among closed forest, edge and canopy gap (Table 8). Growing season evapotranspiration in the edges was 75-98% of that in the closed forest with a lower percentage in MAN than in NAT. In canopy gaps evapotranspiration was 22-30% of that in the closed forest. Annual drainage from the canopy gaps was 76-104% higher than below the closed forest. Annual transpiration in NAT (closed forest) was lower than in MAN. The maximum daily closed forest transpiration in NAT was 2.7 mm (2000) and 2.8 mm (2001) whereas in MAN it was 3.0. Closed forest transpiration was almost identical in NAT between the two years as was also the case for interception loss. Among the annual evaporation components in the closed forest, soil evaporation varied most between years (140-160 mm). Simulated daily closed forest soil evaporation was below 1 mm during most of the simulation period but increased during April and early May where it reached a maximum of 2.3-2.4 mm. The evaporation components differed slightly between NAT and MAN in the closed forest (Table 9). Interception loss was lowest in MAN, whereas transpiration was lowest in NAT. Expressed relative to the maximum canopy LAI (in $mm \cdot m^{-2}$ of $leaf \cdot year^{-1)}$, transpiration is 48 (NAT) and 55 (MAN) and interception loss is 26-28 (NAT) and 24 (MAN).

Discussion

Fluxes in closed forest, edge and canopy gap

In agreement with other studies in temperate forests (Bauhus and Bartsch, 1995; Aussenac, 2000; Gray et al., 2002; Ritter et al., 2005a), this study showed that

while measured SWC in canopy gaps was near field capacity with very little variability during the growing season, it displayed a clear decrease in both edges and closed forests. This coincided with higher drainage fluxes in gaps than in edge and closed forest conditions. Previous research on the same sites as those used in the present study, has demonstrated higher simulated drainage fluxes in canopy gaps than below the closed canopy in a monthly resolution (Ritter et al., 2005b; Ritter and Vesterdal, 2006). For MAN (Ritter et al., 2005b) they were 23% (96 mm) higher in gaps than in the closed forest during a 1 ½ year period (September 2001-April 2003). Further, these authors found drainage fluxes to be low in canopy gaps (7-16 mm in total) in April-August 2002 and to be zero in the closed forest in April-October 2002. In our study, the simulated annual drainage flux was 276 mm (MAN; 87%) and 215-328 mm (NAT; 76-104%) higher in a canopy gap than in the closed forest, thus a relatively large difference between the two categories. In our study, when cumulating the simulated daily drainage flux for each month it was never zero. In the closed forest drainage was < 10 mm $\cdot$ month^{-1} in August-December 2000 and in August-September 2001. For the growing season and at both sites and years the minimum monthly drainage in the gaps was in June (20-32 mm). The annual drainage relative to precipitation was 36-39% (closed forest) and 65-74% (canopy gaps), close to values based on daily simulations in a Central European mixed high elevation forest (Zirlewagen and von Wilpert, 2001, 37% and 61% respectively). Differences for the canopy gaps may be influenced by the relatively small canopy gaps in the study of Zirlewagen and von Wilpert (2001). Only small differences in simulated monthly drainage fluxes were found between canopy gaps and closed forest in mixed stands of silver fir (Abies alba Mill.) and European beech on Central European karst (Vilhar et al., 2005). In our study, periods of low SWC were not well simulated for the canopy gaps leading to a possible overestimation of the drainage flux. However, the large difference in drainage found between gap and closed forest conditions may also result from the specific model application. In contrast to the applications of Ritter et al. (2005b), Vilhar et al. (2005) and Ritter and Vesterdal (2006) this study used a daily time resolution as well as a specific representation of gap microclimate. This may have influenced or magnified the differences between closed forest and gap conditions.

As expected, drainage and evapotranspiration for gap edges were intermediate relative to the closed forest and gap conditions. Drainage in edges relative to closed forest conditions was higher in MAN (35%) than in NAT (7-8%). This

may reflect the abrupt transition from closed forest to gap in MAN in contrast to the gradual transition in NAT where the area classified as edge was relatively large. Though they both represent a point in the forest-gap-transition, estimates of drainage and evaporation should not be used as a general characteristic of edges.

Water budgets in the closed forest

Annual simulated drainage (282-319 mm) was within the range found in other studies of broadleaved forests in Denmark; 197-536 (during 7 years, Ladekarl et al., 2005) and 292 mm (Christiansen et al., 2006). Drainage estimates from simulation studies in Denmark were related to the annual precipitation (Bastrup-Birk and Gundersen, 2004) and the results from our study fit well into the emerging relationship for old deciduous forest with the drainage flux increasing linearly with precipitation. Annual simulated transpiration at our two sites (219-241 mm) was similar to measured transpiration found in other studies but may be lower than most of the reported simulated values. Other simulation studies in temperate deciduous forests have shown 230-365 mm for pedunculate and sessile oak in Denmark (Ladekarl et al., 2005) and 339 mm for Danish European beech (Christiansen et al., 2006). Measured annual transpiration in European beech in Denmark was 204 mm in the period May 5-October 2 (Dalsgaard, 2007b; Dalsgaard, Mikkelsen and Bastrup-Birk, subm.) and in France 218-256 mm (Granier et al., 2000). Interception loss was higher in NAT than in MAN reflecting the differences between the two sites in the parameters governing the canopy storage capacity. The presence in NAT of pedunculate oak and common ash as well as many very old trees with a coarse-textured bark may result in a lower stemflow (Levia and Frost, 2003; Dalsgaard, 2007a). High turbulence increasing the interception loss (Monteith and Unsworth, 1990; Deguchi et al., 2006) caused by the emergence of a few, tall individual trees could have influenced the measured throughfall and stemflow and thereby the simulated interception loss. Transpiration was slightly higher in MAN than in NAT reflecting the higher calibrated value for the maximum stomatal conductance. This implies that the mixed canopy in NAT has a lower canopy conductance per leaf area than the monospecific canopy in MAN. The result may be related to the relatively late leaf emergence for common ash and pedunculate oak and to the observation of low transpiration rates by the ring porous common ash (Hölscher et al., 2005). In North America it was found that for stands composed of both ring porous and diffuse porous tree species, stand transpiration was dominated by the

latter (Oren and Pataki, 2001; Wullschleger et al., 2001). High stand age and low vitality may also contribute to low transpiration rates (Vincke et al., 2005; Delzon and Loustau, 2005).

Model application

We consider the CoupModel as successfully parameterized for the two stands in the closed forest, edge and canopy gaps. However, the model was unable to simulate the moderate decrease in SWC measured in the gaps in mid and late summer. Increasing canopy LAI in the gaps or parameters determining the mean stomatal conductance did not result in improvements. Further, the calibration for the gap edges relied on changes in LAI during the growing season. The development in closed forest LAI followed the observations by Pilegaard et al. (2003) describing an increase in LAI during the growing season. The calibrated changes in LAI for edge conditions (Table 6) tended toward a steeper increase in LAI than in the closed forest. In NAT, early summer LAI increased from 2000 to 2001 possibly reflecting the expansion of roots (Müller and Wagner, 2003) and tree crowns (Muth and Bazzaz, 2002) and changes in the hydraulic conductance of branches (Lemoine et al., 2002). We suggest that the measured course of SWC in gap edges was influenced by water extraction by trees in the closed forest in mid and late summer where soil water availability became low. Similarly we suggest that the moderate decrease in measured SWC in gaps was a result of water extraction by trees in the closed forest and edge. These interactions were not represented in the CoupModel. This would suggest that in this study gap drainage may be slightly overestimated and edge transpiration slightly underestimated. The climate input is important for the simulated water budget and a poor representation of gap soil water dynamics may have been a result of low radiation input in the gap simulation. The level of radiation used in the gap simulations was similar to results found in other studies (Canham et al., 1990). Future improvements in the model application could include an examination of the sensitivity of results to changes in the input climate for gap and edge conditions, regarding the level of input variables as well as their variation in time.

The comparison of simulated and observed SWC in NAT for the 2000 growing season indicated that the closed forest calibration gave a good representation of the processes in the water cycle of this forest. The poor results from the comparison in the canopy gap (Table 7) may be caused by the fact that these

measurements were generally taken at the periphery of the gap and therefore probably more affected by edge trees than the data used for calibration.

Soil characterization and forest floor evaporation

Shortcomings in the soil parameterization were visible at both sites. Deviations between measured and observed SWC may be caused by spatial soil heterogeneity. While an overestimation of SWC_{14} and SWC_{30} was seen for the closed forest in NAT these soil depths were quite well reproduced at the edge. The closed forest SWC may have been influenced by the more sandy soil in the southern part of the measurement plot to a larger extend than the edge and canopy gap (pers. obs.). Further, the decrease in SWC in winter and spring (NAT) is much stronger in the simulations than in the observations for $SWC_{90,}$ indicating that the soil parameterization in this depth may be uncertain. In NAT, measured retention characteristics were variable below approximately 0.5 m depth. Using mean values of soil characteristics in NAT should have introduced only minor errors in the simulated evaporation (Lewan and Jansson, 1996), but for both sites and especially for $SWC_{90,}$ more soil samples and soil profiles as well as measurements of in-situ soil water tension could have improved the soil characterisation (Schelde et al., 1998). The quality of our SWC data may have been influenced by the fact that the TDR measurements rely on the original calibration function developed by Topp et al. (1980) rather than on site-specific calibrations to the soil types at our study sites. TDR measured SWC_{50} and SWC_{90} was within 11% of gravimetrically determined soil water content in NAT (Dalsgaard, 2007b).

While the high estimated porosity of the 3 cm deep organic layer increased the simulated SWC, there is no indication that this caused a general overestimation of SWC. However, this may be a cause for the relatively high soil evaporation found in our simulations (Table 9). In Denmark, young European beech annual simulated soil evaporation was 14% of evapotranspiration (Christiansen et al., 2006) and in oak (Quercus sp.) it was 14-17% (Ladekarl et al., 2005). These two studies did not include soil parameters for an organic layer. In Germany, simulated annual soil evaporation in Norway spruce (Picea abies (L.) Karst.) was 10% of evapotranspiration (Eckersten et al., 1995). While the simulated annual soil evaporation in our study is high, the range of measured (0.1-0.4 mm) and simulated (0.1-0.5 mm) daily soil evaporation (NAT) from three days in late

August 2001 were similar, and measured evaporation values from plots including low vegetation were up to 0.9 mm (Dalsgaard, 2007a). In North America, measured soil evaporation from a mixed deciduous forest (Wilson et al., 2000) was 8.3% of evapotranspiration in the growing season and 15.7% annually in a forest with a LAI of 6.0 $m^2 \cdot m^{-2}$ and lacking forest floor vegetation. In the growing season maximum daily soil evaporation in their study was approximately 0.5 mm and outside the growing season approximately 1 mm. Our estimates are high and may result from an imprecise parameterization for the soil surface, or in the soil evaporation routine of the CoupModel. However, a lower canopy density than in the study of Wilson et al. (2000) and the presence of scattered forest floor vegetation in our stands are both arguments that forest floor evaporation should exceed the rates found in the North American study (Black and Kelliher, 1989; Baldocchi et al., 2000). In a mature declining pedunculate oak stand in Belgium, forest floor evapotranspiration was up to twice as high as the transpiration from the tree canopy (Vincke et al., 2005, canopy LAI 3.1-4.3 $m^2 \cdot m^{-2}$) and with a maximum of 2.9 $mm \cdot day^{-1}$ which is close to our simulated maximum values of 2.3-2.4 $mm \cdot day^{-1}$. Further, forest floor evaporation depends on the moisture content of the litter with an evaporation of up to 0.13 $mm \cdot hour^{-1}$ for wet litter (Wilson et al., 2000). Thus, forest floor evaporation may be expected to vary strongly according to the rainfall frequency. More studies of evaporation from soil, litter and low vegetation in forests would be beneficial.

Conclusions

Simulated water budgets clearly differed between gap and closed forest conditions and the simulated annual drainage in gaps was nearly twice as high as the drainage in the closed forest. The large difference between closed forest and gap conditions may be related to the model application i.e. the daily time resolution and the use of a specific gap microclimate. The model applications for the edge and gap positions were useful for the identification of possible horizontal processes in the water cycle near a gap. Estimates in the water budget of gaps and edges may be influenced by the inability of the model to reproduce these processes. Contrary to expectation we found that the closed forest interception loss was highest for the mixed natural stand whereas transpiration was highest in the monospecific managed stand.

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Tables

Table 1. Stand structure parameters for two broadleaved forest sites in eastern Denmark. Parameters include top height (mean height of the 100 tallest trees ha^{-1}), leaf area index (LAI) and stand basal area (BA).

Stand structure and on-site climate	Suserup Forest (NAT)	Ravnsholte Forest (MAN)
LAI ($m^2 \cdot m^{-2}$) [1]	4.6 (August 24-25, 2000)	4.0 (June 21, 2001)
BA ($m^2 \cdot ha^{-1}$)	40.2	28.5
Species (% of BA)	Fagus sylvatica L. (56)	Fagus sylvatica L. (95)
	Fraxinus excelsior L. (28)	
	Quercus robur L. (13)	
	Ulmus glabra Huds. (3)	
Top height (m)	28.4	28.9
Mean tree height (m) [2]	13.3	23.1
Appr. gap diameter (m)	20	27

[1] Measured 1 m above the ground using the LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA).

[2] Trees > 45 mm stem diameter.

Table 2. CoupModel parameters for two broadleaved forest sites in eastern Denmark. Default values are shown in parenthesis.

CoupModel parameter	Value	Reference
Parameters for the Lohammer equation, other stand properties:		
Height of max. canopy density (0.7)	0.8	Rauner, 1976
Radiation at 50% of max. stomatal conductance, $J \cdot m^{-2} \cdot day^{-1}$ ($5 \cdot 10^6$)	$5 \cdot 10^6$	Persson, 1997
Vpd at 50% of max. stomatal conductance, Pa (100)	359	Jansson et al., 1999
Max. stomatal conductance, $m \cdot s^{-1}$ (0.02)	MAN: 0.0063 NAT:0.0058	Values calibrated in closed forest conditions
Albedo (November-April, June) %	10, 18	Knohl et al., 2003
Water uptake, soil water flow and thermal properties:		
Threshold tension for water uptake, cm water (400)	1000	Christiansen et al., 2006
Flexibility in water uptake (0.6)	0.7	Jansson et al., 1999
Thickness of organic layer, m (0)	0.03	Ritter et al., 2005 Ritter and Vesterdal, 2006
Initial pressure head, cm water (60)	100	

Table 3. CoupModel parameters in closed forest, edge and canopy gap at two broadleaved forest sites in eastern Denmark. Values shown in parentheses are default values.

CoupModel parameter	MAN			NAT		
	Forest	Edge	Gap	Forest	Edge	Gap
Storage capacity for intercepted water:						
Base (0), mm	1	0.05	0	1.1	1.1	0
p_{LAI} (0.2), mm·m^{-2} of leaf	0.1	0.05	0.1	0.2	0.1/0.5[1]	0.2
Reference height:						
Temperature, m	30.9	30.9	2	30.4	30.4	2
Wind, m	57	57	2	57	57	2
Plant structure:						
Growing season LAI, m^2·m^{-2}	2.2 – 4.4	1.1 – 3.3	0.5 - 1	1.4 - 4.6	0.1 - 4.4	0.5 - 1
Rooting depth, m	0.9	0.5	0.5	0.9	0.7	0.7
Height[2], m	28.9	28.9	0.3	28.4	28.4	0.3

[1] 2000/2001

[2] Closed forest and edge: top height. Canopy gaps: on-site observations; Ritter et al., 2005a; K. Hahn and P. Madsen, unpubl. data.

Table 4. Calibration of interception. Regressions of observed (TS_o) vs. simulated (TS_s) values of throughfall + stemflow (mm), NRMSE and R^2-values.

	NAT		MAN
Closed forest:			
Regression	$TS_s = 1.12 \cdot TS_o - 0.97$		$TS_s = 1.01 \cdot TS_o - 0.86$
R^2	0.98		0.98
NRMSE	0.19		0.11
Edge:	2000	2001	2001
Regression	$TS_s = 1.08 \cdot TS_o - 0.75$	$TS_s = 1.16 \cdot TS_o - 1.78$	$TS_s = 0.94 \cdot TS_o - 0.45$
R^2	0.97	0.97	0.98
NRMSE	0.15	0.20	0.14

Table 5. Normalized root mean square error (NRMSE) for the calibration to measured soil water content (SWC). Calibration to observations in 2000 was on June 16- September 1. Calibration to observations in 2001 was on April 24 – August 3. The slope in a linear regression of simulated vs. observed SWC as well as the R^2-value is shown.

	NRMSE				R^2 (slope)	
Depth (cm)	0-14	0-30	0-50	0-90	0-50	0-90
NAT:						
Closed forest 2001	0.23	0.10	0.04	0.14	0.99 (0.92)	0.99 (0.98)
Edge 2000	0.11	0.05	0.07	0.11	0.97 (0.87)	0.92 (0.73)
Edge 2001	0.15	0.09	0.14	0.16	0.98 (0.94)	0.99 (0.90)
Canopy gap 2000	0.23	0.11	0.06	0.05	0.89 (0.85)	0.89 (1.03)
Canopy gap 2001	0.20	0.10	0.09	0.12	0.13 (0.34)[1]	0.01 (0.09)[1]
MAN:						
Closed forest 2001	0.04	0.09	0.07	0.12	0.97 (0.99)	0.99 (1.04)
Edge 2001	-	0.13	0.17	0.25	0.94 (1.05)	0.96 (1.09)
Canopy gap 2001	0.02	0.08	0.03	0.12	0.72 (0.98)	0.58 (0.98)

[1] The low R^2-values and slopes were obtained for the entire period April 24-August 3, 2001. For the early summer (April 24 - June 1, 2001), R^2-values were 0.90 and 0.97 and slopes were 0.72 and 0.71 for 0-0.5 and 0-0.9 m depth respectively. After June 1 until August 3, 2001 R^2-values of 0.78 and 0.40 and slopes of 0.54 and 0.39 were found for 0-0.5 and 0-0.9 m depth respectively.

Table 6. Initial and final estimates of leaf area index (LAI, $m^2 \cdot m^{-2}$) for simulations in edge positions in two canopy gaps.

Day	May 7	June 1	July 1	August 1	October 1
Initial LAI:					
NAT	0.7	1.4	2.1	2.3	2.1
MAN	1.1	1.5	2.0	2.2	2.0
Final LAI:					
NAT 2000	0.1	0.1	0.1	4.4	3.1
NAT 2001	0.1	1.4	2.1	4.4	3.1
MAN	1.1	2.3	3.0	3.3	3.0

Table 7. Normalized root mean square error (NRMSE) for a comparison of simulated SWC and measurements of SWC from positions not used in the model calibration for Suserup Forest (NAT). The R^2 -value and slope of a linear regression of simulated vs. observed SWC is shown. The number of observations is 19, 9 and 3 for closed forest, edge and gap respectively.

	NRMSE				Slope				R^2			
Depth (cm)	0-14	0-30	0-50	0-90	0-14	0-30	0-50	0-90	0-14	0-30	0-50	0-90
June 16, 2000 - April 19, 2001:												
Closed forest	0.30	0.22	0.21	0.12	1.11	1.01	1.10	1.20	0.84	0.81	0.83	0.88
Edge	0.19	0.14	0.16	0.08	1.02	0.90	0.89	0.96	0.82	0.81	0.78	0.74
Canopy gap	0.48	0.31	0.28	0.14	0.52	0.61	0.56	0.29	0.52	0.64	0.48	0.20
June 16 – Sept 1, 2000:												
Closed forest	0.23	0.12	0.09	0.15	1.24	0.83	0.84	0.86	0.89	0.88	0.94	0.89
Edge	0.14	0.10	0.10	0.07	0.90	0.80	0.79	0.89	0.82	0.92	0.96	0.99
Canopy gap	0.45	0.27	0.21	0.11	0.75	0.67	0.66	0.71	0.70	0.77	0.75	0.74

Table 8. Simulated annual and growing season output (mm) for closed forest, edge and gap conditions for two broadleaved forest sites in eastern Denmark. Precipitation (P) and the calculated Makkink potential evapotranspiration[1] (E-pot) is also shown (mm).

	NAT 2000			NAT 2001			MAN 2001		
	Closed forest	Edge	Canopy gap	Closed forest	Edge	Canopy gap	Closed forest	Edge	Canopy gap
May-October:	P: 373			P: 551			P: 485		
	E-pot: 403			E-pot: 448			E-pot: 424		
Interception	120	94	39	129	162	78	104	16	24
Transpiration	218	129	15	216	158	14	238	195	23
Soil evaporation	75	115	36	70	87	33	76	105	57
Evapotranspiration	414	339	90	415	408	125	419	316	103
Drainage	80	92	231	128	136	390	84	162	361
Annual:	P: 766			P: 873			P: 813		
	E-pot: 510			E-pot: 544			E-pot: 520		
Interception	140	112	122	144	179	146	117	17	90
Transpiration	220	130	15	219	160	14	241	197	23
Soil evaporation	160	200	89	140	157	80	147	175	106
Evapotranspiration	519	443	226	502	496	239	505	390	219
Drainage	282	305	497	316	337	644	319	431	595

[1] Calculated as in Rosenberg et al., 1983; Plauborg et al., 2002, Scharling and Kern-Hansen, 2002).

Table 9. Evaporation components from simulations in closed forest conditions for two broadleaved forest sites in eastern Denmark. Given as percentages of evapotranspiration; annually and for the growing season.

	Annual			May-October		
% of	NAT	NAT	MAN	NAT	NAT	MAN
evapotranspiration	2000	2001	2001	2000	2001	2001
Interception	27	29	23	29	31	25
Transpiration	42	44	48	53	52	57
Soil evaporation	31	28	29	18	17	18

Figures

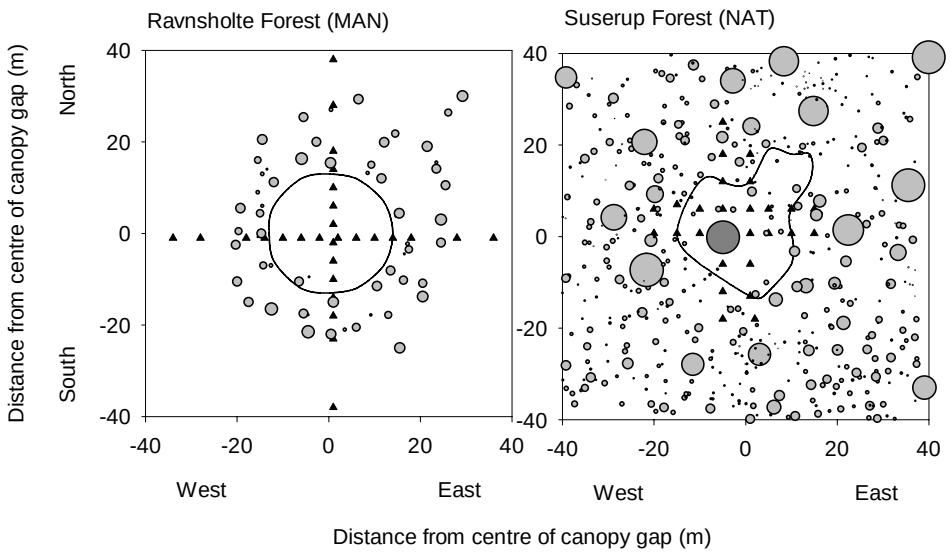


Figure 1. SWC and throughfall measurement positions (black triangles). The lines indicate the edges of the gaps. Gray circles show the positions of individual trees near the gaps. The canopy gap in NAT was created when a number of trees uprooted and one large old tree lost most of its crown. This tree is shown with the dark gray circle. The stem and a few branches are still present.

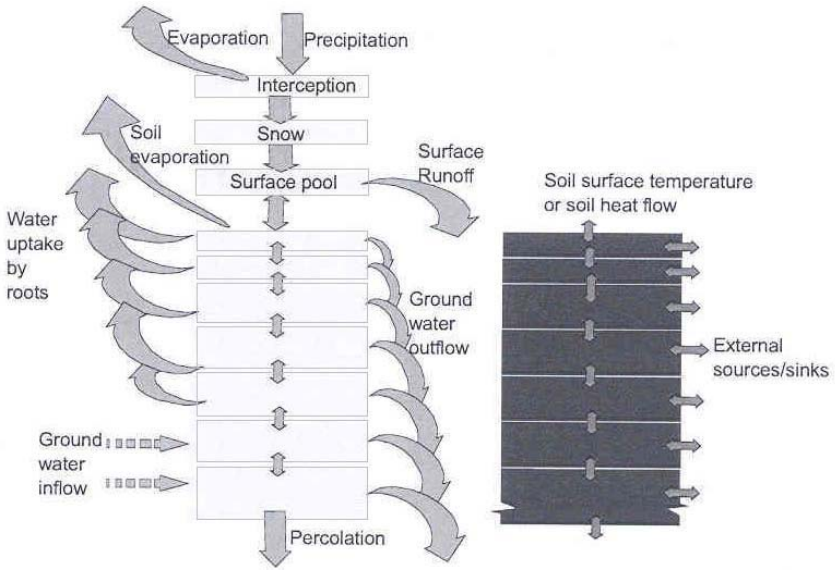


Figure 2. Mass balance (left) and heat balance (right) of the CoupModel (Jansson and Karlberg, 2004).

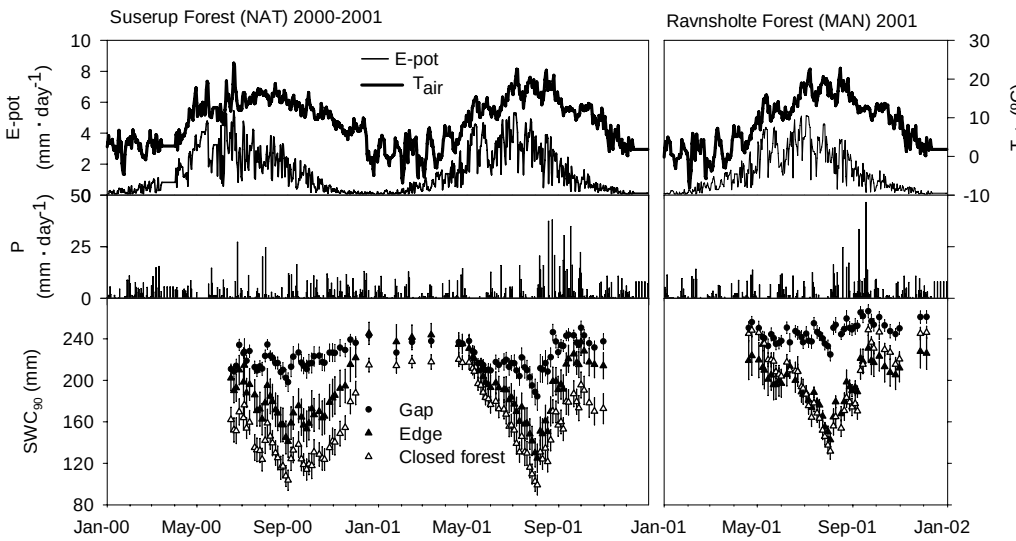
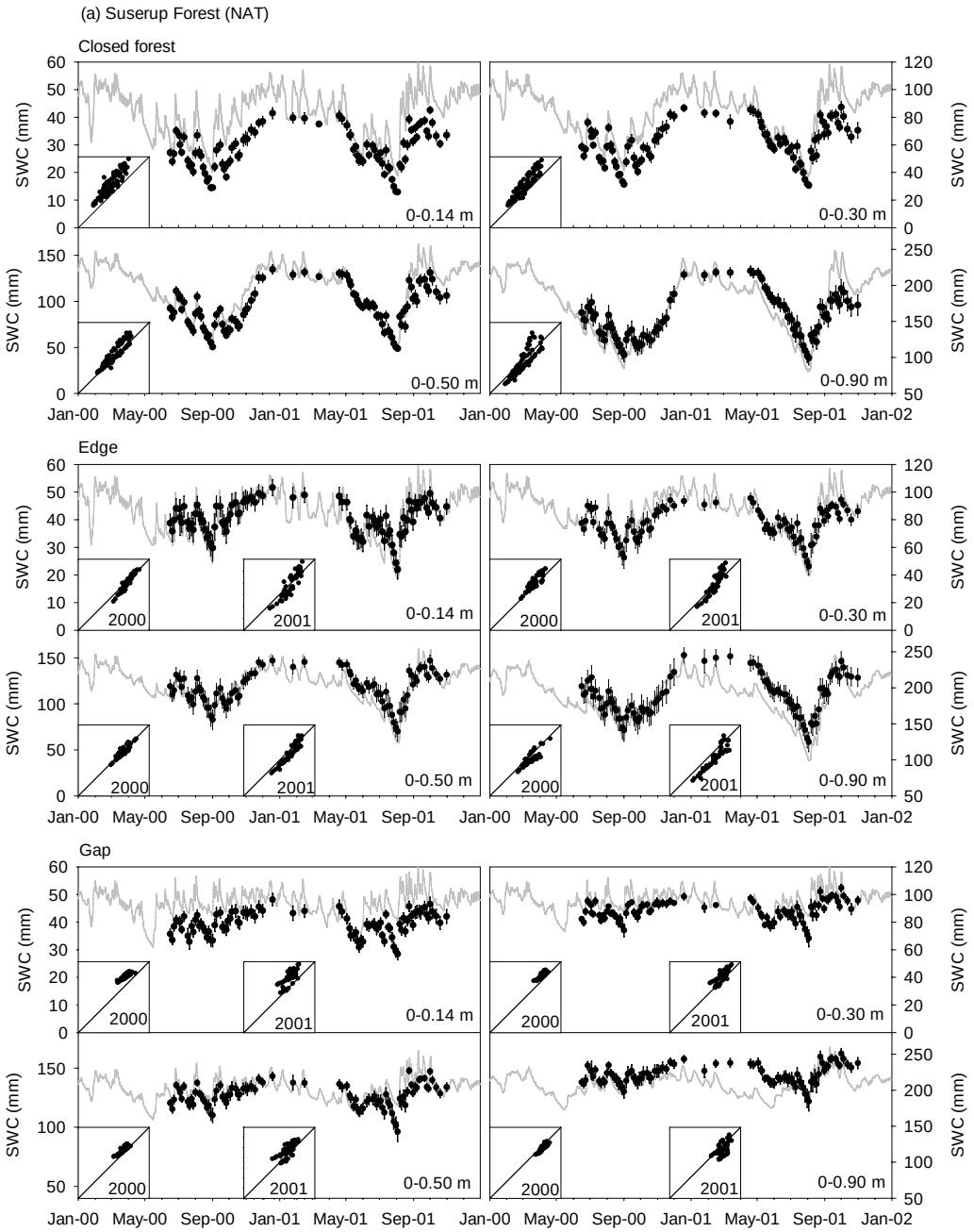


Figure 3. Makkink potential evapotranspiration (E-pot), daily mean air temperature (T_{air}), daily precipitation (P) and measured soil water content in 0-0.90 m depth (SWC_{90}) in Suserup Forest 2000-2001 and Ravnsholte Forest 2001. SWC_{90} is shown for the gap, edge and closed forest positions. Error bars show ± one standard error of the mean.


(a) Suserup Forest (NAT)
Closed forest
Edge
Gap
SWC (mm)
0-0.14 m
0-0.30 m
0-0.50 m
0-0.90 m
2000
2001
Jan-00
May-00
Sep-00
Jan-01
May-01
Sep-01
Jan-02

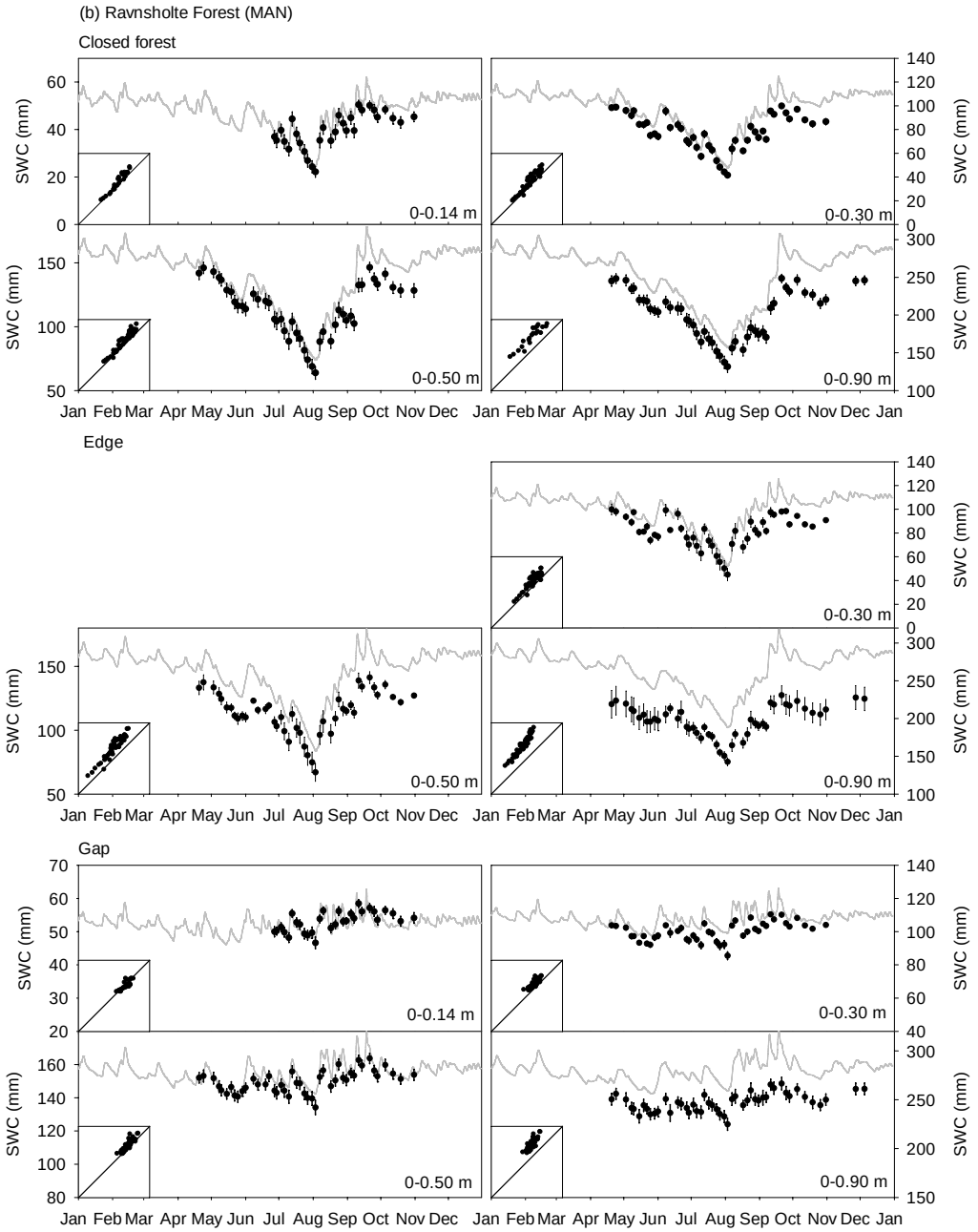

(b) Ravnsholte Forest (MAN)
Closed forest
Edge
Gap
SWC (mm)
0-0.14 m
0-0.30 m
0-0.50 m
0-0.90 m
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan

Figure 4. Measured and simulated SWC in closed forest, edge and gap in (a) Suserup Forest (NAT) and in (b) Ravnsholte Forest (MAN). Inserts are 1:1 plots of simulated vs. observed SWC using the same axis range as the time series. Error bars show ± one standard error of the mean.

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